IX. *On the Structure and Affinities of* Heliopora cœrulea, Pallas. *With some Observations on the Structure of* Xenia *and* Heteroxenia.

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[Plates 10–13.]

Although the structure of *Heliopora* has been the subject of a careful memoir by the late Professor H. N. Moseley, a renewed examination of this interesting and isolated Alcyonarian has, for many reasons, seemed to me to be desirable. There are questions relating to the structure and formation of the hard parts which were not conclusively settled by Moseley's paper, and the great increase of our knowledge of the anatomy of other Alcyonaria has rendered it necessary to overhaul all older work in the light of more arecent researches. Professor Moseley himself was anxious that the genus should be re-examined, and, some time before his death, he pressed me to commence work on some specimens which I had brought back with me from Diego Garcia.

The material which I have used in the course of my work consisted of the above-mentioned spirit specimens from Diego Garcia, of the fragments of the specimens which served Professor Moseley for his original memoir, and a well preserved portion of a colony, which Dr. S. J. Hickson brought from Talisse, and gave to Professor Lankester, who kindly handed it over to me for examination. This specimen of Dr. Hickson's was most useful, because the growing tips of the colony were preserved uninjured, and I was therefore able to make sections illustrating the structure at the point where most active growth takes place. Of dried specimens, I have had a large collection, including my own from Diego Garcia, Dr. Hickson's from Celebes, and a number of specimens from the collection of the late Mr. George Brook, which Mrs. Brook has been kind enough to hand over to me, together with a rich and varied collection of other Anthozoa. Unfortunately the labels have become detached from most of the specimens, but those that remain show that the corals formed part of the collection made by Professor Haddon in Torres Straits.

All the specimens in my possession belong to the same species, *Heliopora cærulea*,

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PALLAS, which is the only living species known. With one exception, they all show the same habit of growth, viz., broad, upright, lobed or digitate masses flattened from side to side. The exception is a specimen from Mr. BROOK'S collection, in which the colony is more explanate, forming an encrustation over an older dead colony, and produced on its upper surface into numerous short, thick, lobed or subramose projections, which are sub-circular or sub-oval in section, and are not laterally compressed. The appearance of the colony differs so markedly from that of the more common form, that I thought that it must be a new species, but after careful examination I was unable to find any special characters in the calicles or in the echinulations which would warrant its separation from other forms. It is evidently identical with DANA'S *H. tuberosa*.

The most recent figures of *Heliopora* are those given by SAVILLE KENT (6) in his work on the Great Barrier Reef of Australia, but they are far inferior to those of MOSELEY, and are not so good as the old figures of MILNE-EDWARDS and HAIME (13). There is one interesting point in his figures and description; he has seen and figured the expanded polyps, which MOSELEY failed to do, and I was equally unsuccessful at Diego Garcia.

The tentacles are seen to be of the usual Alcyonarian type, *i.e.*, pinnate, though the numbers of the rows of pinnæ and other details are not given. Before I saw SAVILLE KENT'S figure I had been led to the conclusion that the tentacles, which as MOSELEY pointed out, are introverted when the polyp is retracted, were simple and not pinnate. I have been unable to find any trace of pinnæ in any of my sections, and both in them, and in MOSELEY'S figures and description, there is only evidence of plications in the ectoderm of the introverted tentacles, which may indicate the pinnæ, but might equally well be attributed to contraction in spirit.

The structure of the corallum in *Heliopora* is so intimately connected with that of the polyps and cœnenchymal cæca that I shall reverse the usual order of description and begin with the soft tissues.

On decalcification soft tissues are seen to form a sheet, covering the whole of the surface of the corallum; they penetrate but a very little way into its interior. The tissues on one face of the colony are not in any way connected with those on the opposite face of the colony, excepting in so far as they are continuous at the edges of the fronds. Hence the axial part of the skeleton is destitute of living tissue.

In fig. 1 I have given a diagrammatic representation of a portion of the layer of soft tissues, including an expanded polyp, which explains better than any description could the structures of which it is composed and their relations *inter se*. The polyp is represented as expanded; I have not seen an expanded polyp, and am not able to vouch for the accuracy of this part of the figure, the character of the tentacles and pinnæ being founded on SAVILLE KENT'S description and drawing. The ectoderm (*ec.*) covers the whole surface of the colony, and completely closes it in, except where the mouths of the polyps afford a means of communication to the interior. This

layer of ectoderm is continuous with the ectodermic layer of the exsert moieties of the polyps, and at the lips of the mouths of the latter, passes into the ectoderm lining their stomodæa.

In the fully developed parts of the colony there is, beneath the ectoderm, a thin layer of mesoglœa, which passes into the mesoglœa of the polyps and into that of the cœnenchymal tubes.

Each polyp may be regarded as consisting of two parts, an exsert moiety (fig. 1, P′) and an inner moiety which occupies the cavity of the calicle. The general structure of the polyp is of the normal Alcyonarian type, and has been so fully and accurately described by Moseley that no further account of it is necessary. The structures known as cœnenchymal cæca (fig. 1, *c.t.*) are peculiar to *Heliopora*. Their relations may be understood by a comparison of figs. 1 and 2. The inner moieties of the polyps are placed in direct communication with adjacent cœnenchymal cæca, and in indirect communication with one another by a network of canals which lies at the surface of the colony, just beneath the investing layer of ectoderm and mesoglœa. This network, which I shall call the superficial canal system, takes its origin from the polyps just below the point where the ectoderm of the latter passes into the ectodermic sheet which covers the surface of the colony. From this region canals lined with endoderm, generally to the number of 15 or 16, are given off from each polyp; they branch and anastomose after a very short course to form a tolerably regular network, from the nodes of which the cœnenchymal cæca project inwards at right angles to the surface of the colony, and therefore at right angles to the plane in which the network of superficial canals lies. A surface view of a decalcified portion of a colony of *Heliopora* is given in fig. 2. The external covering of ectoderm has been stripped away, and the network of superficial canals is very well seen, the cœnenchymal cæca being represented by the dark areas at the nodes of the network. The spaces between the cœnenchymal cæca and between these and the polyps are occupied by calcareous tissue, and the echinulations with which the surface of the corallum is studded project through the meshes of the network of superficial canals and touch the ectoderm.

The calcareous tissue is deposited by a special layer of cells, described by Moseley as connective tissue cells, and as being "mesodermic." These cells, the characters of which I will describe further on, completely invest the cœnenchymal tubes, the inner moieties of the polyps, and the inner parts of the superficial canals, *i.e.*, those parts which are not overlaid by the sheet of external ectoderm. As the superficial canals and the cœnenchymal tubes are lined throughout by endoderm, we find that the whole of these structures consist internally of a layer of endoderm, outside this a thin layer of mesoglœa, and outside this again a layer of coral-producing cells, which I shall call *calicoblasts*. The question is, what is the nature of these calicoblasts and from what layer are they derived? They are certainly not "mesodermic," as Moseley described them, for they lie wholly outside the mesoglœa and are not

imbedded in it as are the spicule-forming cells in so many Alcyonaria. This at least is true of the older parts of the colony where active growth has ceased.

Since the publication of MOSELEY'S paper the mesodermic, or, as I should prefer to call it, the mesoglœal nature of the skeleton, has not been called into question, excepting by G. VON KOCH, who, in the introductory chapter to his work on the Gorgonidæ (8) suggests, with his usual acumen, that the skeleton of *Heliopora* may probably be ectodermic. I have succeeded in proving that this is, in fact, the case. The minute structure of the parts whose relations have been described above, are best studied in sections made vertically to the surface of the colony. Such a section, taken from the growing tip of a frond, is represented diagrammatically in fig. 3, and a portion of the same section, more highly magnified, is given in fig. 4 (Plate 10). Many of the histological features have already been accurately described by MOSELEY, but as he appears to have overlooked the origin and significance of the calicoblasts it will be necessary for me to recapitulate. There is some difference between the structure as seen at the growing tips of the colony and that of the older parts. I will begin by describing the former, and will refer to the older parts later on.

The superficial system of transverse canals, which forms so characteristic a part of the structure of the older parts of the colony, is not recognizable as such in the growing edges. One finds instead, that the external ends of the cœnenchymal cæca are closely apposed to one another above the limits of the skeleton, and their cavities are often completely shut off from one another; when they do communicate, it is by means of short irregularly disposed passages. The upper ends of the cœnenchymal cæca are rarely simple, but generally produced into several short diverticula. These relations are shown diagrammatically in fig. 3, and a smaller part of the same section is shown under a higher power in fig. 4.

It is to be observed in fig. 4, that in the most superficial part of the section the mesoglœa is not a distinct structureless lamella lying between the ectoderm and endoderm, but that its place is taken by an ill-defined gelatinous substance in which cells and cell processes are visible, and that here and there endoderm cells and cavities, lined by endoderm (fig. 4, *ed.c.*), have pushed their way into it.

The ectoderm is clearly the active layer in the process of growth which proceeds rapidly at the growing edge. It consists, as may be seen in fig. 4, of a single layer of cells, for the most part elongate and pyriform, the broader outer ends of which rest on a well defined external limiting membrane. It is evident that the ectoderm cells are proliferating rapidly. Their inner ends are produced into blunt processes, which are more granular and stain less deeply than the external parts. These interior processes are eventually separated off as fusiform cells, which, for some time, retain their connection with the ectoderm cell from which they originated, by means of fine protoplasmic processes. Some of these cells increase in size, become more granular, apply themselves to the mesoglœal lamina of the deeper parts of the cœnenchymal tubes, and secrete the calcareous skeleton; these are calicoblasts (*cal.*, fig. 4), of

whose ectodermic origin there can be no doubt, as they may, in many places, be traced into direct connection with the ectoderm cells from which they originated. At one period, however, the calicoblasts are scarcely to be distinguished from other fusiform cells similarly derived from the ectoderm, which form the structureless mesoglœa, and eventually break up and disappear.

These fusiform cells separate from the ectoderm, they appear to lose their definite outline, they become finely granular and stain less readily than before, a gelatinous substance makes its appearance between them, and eventually they become disintegrated and are entirely used up in the formation of a homogeneous mesoglœa. In some places it appears as though, by an abbreviation of this process, the inner ends of the ectoderm cells themselves, without becoming detached, change in character, stain less readily than the external parts, and become dissolved, as it were, in the course of the formation of a structureless substance from them. Such a mode of formation of the mesoglœa is identical or nearly so with the process described by WILSON in the developmental history of *Renilla* (19).

It results then, from the activity and division of the ectoderm, that an ill-defined gelatinous layer of some thickness is formed below it, and that special cords of cells penetrate inwards beyond this and become skeleton-producing cells or calicoblasts.

The thick gelatinous mesoglœa lying immediately below the ectoderm is penetrated by cords and groups of cells which grow into it from the endoderm, as well as by direct hollow outgrowths of the cœnenchymal cæca. The cords or groups of cells soon acquire a lumen (see fig. 4, *ed. c.*), and continue to increase rapidly in size, eventually forming new cœnenchymal tubes which grow upward, accompanied by the direct outgrowths of the preexisting cœnenchymal cæca. As these two sets grow outwards they push the ectoderm before them, and the process of new formation of mesoglœa and calicoblasts from the ectoderm, with the ingrowth of endodermic offsets into the freshly-formed mesoglœa is constantly repeated. It is to be observed that, as a result of this mode of growth, the number of the cœnenchymal cæca is constantly increasing at the upper edge of the colony. As the cells from which the mesoglœa is formed and those which become calicoblasts are derived in the same manner from the ectoderm, and are at first indistinguishable from one another, it might be argued that the calicoblasts are not ectodermic, but are merely specialized mesoglœal cells. I do not think, however, that this view will recommend itself to anyone who carefully examines fig. 4. From the time that they are separated from the ectoderm the two sets of cells take up definite positions apart from one another. Those nearest the endoderm are specially concerned in the formation of mesoglœa, those further from the endoderm early arrange themselves in a definite layer which clothes the mesoglœa after its formation. It is only where the mesoglœa is in course of formation that the two are indistinguishably mixed together. The primitively thick gelatinous mesoglœa soon shrinks. It looks as if it were encroached upon and reduced as a consequence of the growth of the endodermic canals on one

side, and of the formation of the skeleton as a result of the activity of the calicoblasts on the other. Thus in the deeper parts of the section it appears as a very thin lamella lying between the endoderm and the calicoblasts, in which no structure and no traces of cells are recognizable. I will show in the latter part of this paper that there are other Alcyonarians besides *Heliopora* which have an ectodermic skeleton, with this difference, that in their case the skeleton is spicular and discontinuous. *Heliopora* is the only recent example of an Alcyonarian with a solid lamellar skeleton.

In his description of the soft parts of *Heliopora*, MOSELEY has described a superficial and a deeper canal system as underlying the surface of the colony. MOSELEY'S deeper or transverse canal system is what I have described as the superficial network. It is only present as such in the older parts of the colony, and where it is established there is no trace of those further outgrowths described by MOSELEY as his superficial canal system. These are present only in the growing edges of the fronds, where the transverse network is not established. The transverse network is formed at the sides of the colony where active growth ceases to take place. The above-mentioned outgrowths from the outer ends of the cœnenchymal cæca meet and coalesce over the walls separating one cæcum from another. In the spaces left between the communicating canals thus formed the calicoblasts push their way, and form calcareous deposits which project above the level of the mouths of the calcareous tubes as the spines which decorate the surface of the corallum. It results that the canals of the transverse network lie in the depressions between contiguous spines.

The endoderm does not call for special mention. It is crowded with Zooxanthellæ, which are more numerous in the superficial canals and in the outer ends of the cœnenchymal cæca than in the deeper parts.

The nematocysts of *Heliopora* are, as far as I have been able to determine, confined to the ectoderm of the polyps, and are not found in the ectoderm covering the remainder of the surface of the colony. They are, as MOSELEY has described, exceedingly minute, and their structure is difficult to make out, but my observations agree with his in all respects.

The Corallum.—In a dried specimen of *Heliopora*, which has been well macerated in caustic potash, two sets of superficial apertures are observed; larger irregularly scattered calicles, and minute cœnenchymal fenestræ which surround them. A third set of apertures is due to the inroads of the parasitic worm Leucodora. It need hardly be explained that the cavities in the corallum correspond with the polyps and cœnenchymal cæca, the interstices between these latter being occupied by the hard tissues.

If one of the flat fronds of *Heliopora* is fractured vertically, its central portion is seen to be formed of a number of more or less parallel vertical tubes; in transverse section these tubes are seen to have thin walls and to be irregularly polygonal, from mutual pressure. These vertical tubes, after an upward course of greater or less

extent, bend sharply outwards, taking a course at right angles to the surface of the colony, on which they open as the above-mentioned cœnenchymal fenestræ. The cavities of the tubes are interrupted from place to place by flat or shallow saucer-shaped partitions, the so-called tabulæ, and their walls, after they have bent outwards towards the surface, are thickened by a secondary deposit of carbonate of lime. In the oldest parts of the colony this secondary deposit is sometimes of such thickness as to entirely fill up the cavities. In and among the tubes are seen the larger calicles, which are formed by the arrest in growth of several contiguous tubes (fig. 10), whilst those surrounding them continue to grow outwards, as has been described by MOSELEY. The calicles are of very various depth. Some of them are only superficial, and in the fresh condition are entirely occupied by the polyps belonging to them. Others reach for some depth into the colony, and their cavities are interrupted, like those of the cœnenchymal tubes, by tabulæ, but in no case does a calicle extend into the vertical system of central tubes; it is always more or less horizontal and perpendicular to the surface of the frond. As the tubes in their deeper vertical course are thin walled, and in their outer horizontal course are thick walled, a frond may readily be split into right and left halves, and this often happens if it is roughly broken across. The vertical tubes gain the surface at the growing tips or edges of the fronds. In these places the corallum is of less dense and more delicate structure than in the older parts of the colony; a surface view of a portion of a growing edge is represented on a large scale in fig. 5. The mouths of the tubes or cœnenchymal fenestræ, as we may call them, are seen to be most irregular both in shape and in arrangement. They are generally irregularly quadrilateral, more rarely pentagonal or hexagonal. New tubes are formed in the angles where the walls of the older tubes unite, and at first are triangular in section, but as growth proceeds they become quadrilateral and eventually polygonal. Irregular as is the arrangement of the mouths of the tubes, they show a tendency to form in places little concentric systems, usually consisting of a central tube surrounded by eight others. Such a system is well shown in the left-hand lower corner of fig. 5. New calicles appear to originate among the cœnenchymal tubes by the arrest in growth of the tubes composing such a concentric system. The walls of the new calicle are formed by the adjacent tubes and the partitions which separate the latter from one another, grow inwards into the newly formed calicle, and form the pseudosepta, which, as may be seen in fig. 5, are at first irregular and rudimentary. Thus the floor of a newly formed calicle opens below into a limited number, generally nine, of cœnenchymal tubes, but as growth proceeds a tabula is formed across the cavity of the calicle, and it is completely closed below.

In the older parts of the colony the calicles and cœnenchymal tubes present an appearance very different from that of the growing fronds. Drawings of a surface view of the skeleton of *Heliopora* have already been given by MILNE-EDWARDS and HAIME, and by MOSELEY, but I have thought it worth while to give a large-scale

drawing of a portion of a colony, the details of which have been carefully drawn with the camera lucida, which represents more accurately the exact features of the skeleton. A comparison of this figure with fig. 1 and with fig. 2 will show the relations of the corallum to the soft tissues.

In the older parts of the colony the walls of the cœnenchymal tubes are much thicker, and the diameters of the tubes are correspondingly reduced. The arrangement of the tubes appears to be more regular than at the growing edges, but no regular symmetry of growth is recognizable, such as has been described by MOSELEY in a quickly-expanding frond (*loc. cit.*, p. 100). Such a regular arrangement of the fenestræ in straight or curved lines radiating towards the points of extension is only to be seen in places where very rapid growth has taken place, and in such places there are few or no calicles. Wherever calicles are formed there is a tendency for the cœnenchymal tubes to form concentric systems around them, but the symmetry of one system is destroyed by its overlapping an adjoining system, and such an irregular arrangement as is shown in fig. 6 results. It may be seen that the walls of the cœnenchymal tubes are not always complete, so that two or more tubes may open freely into one another, forming irregular clefts in the surface.

Viewed from above, the skeleton enclosing the cœnenchymal cæca of *Heliopora* appears to form a network, of which the meshes correspond to the nodes in the network of superficial canals above described, and the nodes correspond to the meshes of the superficial canals. In the skeleton, the nodes are produced into stout spines, which project through the meshes of the superficial network of canals and extend to the ectoderm, the canals themselves passing from tube to tube in the depressions between the spines.

The pseudosepta, which are prominent in the older calicles, are really the overgrown spines of the tubes adjacent to the calicle. MILNE-EDWARDS and HAIME described twelve septa in *Heliopora;* MOSELEY gives twelve as a common number, but says that it is subject to great variation, as many as sixteen being sometimes present. In his figure, fifteen pseudosepta are drawn. In all the specimens which I have been able to examine, fifteen is the common number in the adult calicles. In incomplete calicles, twelve, ten, or even as few as eight, may be present; but, as growth proceeds, the number fifteen is generally completed. I have attempted in various ways to give an explanation of the constant recurrence of this number, but have not been successful. Were the cœnenchymal tubes symmetrically distributed, either in a quincunx or in parallel rows, the entire suppression of groups of seven and the arrest of growth of the inner walls of twelve tubes surrounding each group, would leave the walls of adjacent tubes projecting as twelve pseudosepta into the cavity thus formed. In *Heliolites* the pseudosepta are constantly twelve in number, and their presence appears to result from this mode of formation; but in *Heliopora* the explanation is more difficult, and has baffled me. It is obvious that there is no homology between

the pseudosepta of such Alcyonarian corals as *Heliopora* and *Heliolites* and the septa of the Madreporaria—a fact which has already been pointed out by MOSELEY.

As regards the minute structure of the corallum, in many points I have not been able to make my observations agree with those of MOSELEY, and I have been quite unable to reconcile his fig. 4 with any of my sections. According to him, the skeleton is composed of a number of rods which are vertically disposed to the surface of the colony, and are Y-shaped in section. The cœnenchymal tubes are formed by the union of the arms of the Y's one with another, and he figures distinct sutures where the union takes place.

I have given careful drawings in figs. 7 and 8 of a tangential section of a growing edge of a colony, at a stage corresponding with fig. 5, and of a section parallel with the surface of an older portion, corresponding with fig. 6. The hard tissues at the growing tips are extremely fragile, and it is difficult to make a section thin enough to display the structure without breaking it up altogether. I was successful only after several attempts. In the growing edge, the walls of the cœnenchymal tubes are seen to be composed of numerous flat laminæ of calcareous tissue, each with its own centre of calcification. In transverse section, these laminæ look like thin trabeculæ, united one with another to form a network in the following manner. At each node three trabeculæ meet, and are united by sutures to form a Y, and each arm of the triradiate figure thus produced, unites with an arm of an adjacent triradiate figure, and thus a more or less regular network is produced. In some cases, a single trabecula is common to two adjoining Y's, and in other cases the uniting limbs of adjacent Y's are so short that they become confluent, and so produce irregularities in the arrangement.

Were the union between the lamellæ perfectly regular, as above described, a sort of honeycomb structure would result, all the cells of which would be regular hexagons, and the walls of each would be composed of twelve separate lamellæ, common to the cell and the six adjacent cells. As is shown in figs. 5 and 7, no such regularity is traceable in *Heliopora*, but the section shows that the fundamental plan of structure tends to this result. In *Heliolites* the cœnenchymal tubes or cells are nearly regularly hexagonal, and the arrangement may fairly be called typical. It is worth remarking here that the constant number of twelve pseudosepta in *Heliolites* is the necessary result of the formation of the calicles by the suppression of a group of seven central cœnenchymal tubes and the arrested growth of the adjacent walls of the twelve cells surrounding the group (see diagram, fig. 9, Plate 11).

In *Heliopora*, the union between the lamellæ which form the walls of the cœnenchymal tubes becomes intimate at an early period, and the sutures which show where two such lamellæ have united, are visible only in the extremities of the growing fronds. In the deeper parts of the corallum they are altogether obliterated.

In the centre of a colony, where the tubes take a more or less vertical course, no appreciable thickening of the walls of the tubes takes place, and they retain their polygonal shape. But where they bend outwards to reach the surface at the sides of

the colony, there is a considerable secondary deposit of carbonate of lime, both in the cœnenchymal tubes themselves and in the calicles. This deposit is due to the activity of the calicoblastic cells which form the outer walls of the cœnenchymal cæca and of the insert moieties of the polyps, and has the form, in the cœnenchymal tubes, of a ring-shaped deposit, which may attain to such a thickness as to almost entirely obliterate the lumina of the tubes. In the case of the calicles, the secondary deposit appears to start from several centres of calcification, usually six in number in the deeper parts of the calicles. A section of an older part of the corallum is given in fig. 8. In the left hand upper corner, a portion of a calicle is shown with the secondary deposit formed from its separate centres of calcification, and in the cœnenchyme the lumina of the tubes are seen surrounded by rings of calcareous deposit, between which the original first formed walls of the tubes are still distinctly recognizable.

The deep blue pigment, to which the colony owes its characteristic colour, is not diffused uniformly throughout the corallum, but is confined chiefly to the circumferences of the secondary deposits. When viewed by transmitted light the primary part of the skeleton, *i.e.*, that part which was first laid down in the growing edge of the frond, and corresponds to fig. 7, appears yellowish-white, and the growing tips themselves are almost destitute of blue colour. A faint band of blue may, however, be distinguished at the edges of each lamina, even in such a section as is shown in fig. 7. In the older parts the secondary ring-like deposit appears faintly blue internally, but there is a deep blue ring externally, at the point where it is united to and fused with the primary laminæ. In the lower part of fig. 8 I have indicated this localization of the pigment by dark shadow.

As regards the colouring matter, on which some investigations have been made by MOSELEY, I have found that the blue colour of the corallum is unaltered by prolonged treatment with hot caustic potash or alcohol. When the coral is decalcified in strong hydrochloric acid, the colouring matter, as observed by MOSELEY, is set free. On filtering the blue colouring matter remains on the filter and the filtrate has a very faint blue tint, not a greenish tint as MOSELEY writes. If now the blue matter on the filter paper be thoroughly washed with distilled water, and afterwards collected and dried, it is insoluble in ether and alcohol and in carbon bisulphide. It is readily soluble in weak solutions of ammonia and caustic potash, giving grass-green solutions, which fade to yellow after prolonged exposure to direct sunlight. Treatment with strong nitric acid gives a violet solution which soon becomes dirty yellow. The dried blue residue from the filter paper ignites readily and leaves behind a very small amount of colourless ash, showing that the pigment is organic. MOSELEY has stated (14) (p. 103) that the blue colouring matter is dissolved at once off the filter by alcohol, giving an intensely blue solution very like that of copper sulphate in colour. This is not true in cases where the residue has been thoroughly washed with distilled water till all traces of acid are removed. It is then insoluble

in alcohol, but if the alcohol be slightly acidulated with hydrochloric acid the blue solution described by MOSELEY is obtained. MOSELEY must have washed the filter paper with alcohol before removing the last traces of acid used in decalcification.

The blue colouring matter is insoluble in ether even after the addition of acids or alkalies, but it dissolves readily in alcohol to which two or three drops of a 30 per cent. solution of caustic potash have been added, giving the dirty-green solution described by MOSELEY.

The acid alcoholic solution gives the spectrum described by MOSELEY. The violet end of the spectrum is absorbed as far as G, at the other end the absorption extends as far as 55, which is somewhat less than the amount given by MOSELEY. In the green solution produced by treatment with caustic soda the absorption of the violet and blue extends as far as 47, that of the red to 66. I have not been able, for want of time, to extend my observations on the colouring matter of *Heliopora;* the violet reaction with nitric acid suggests some affinity with murexin, from which however it differs in other characters.

As regards the mode of growth and architecture of the colony, I am unable to agree with the account given by MOSELEY and illustrated by his figure, Plate 9, fig. 15. He assumes the existence of a mother polyp which grows vertically upwards, giving off lateral buds or stolons, which subdivide repeatedly and give rise to cœnenchymal cæca, amongst which calicles are here and there formed by the suppression of a limited number of tubes. The explanation is ingenious, but it is controverted by the fact that there is not, in any colony, any trace of such a central apical polyp, and a study of the colony, especially of its central layer and of its growing edge, shows most convincingly that the cœnenchymal cæca are the active agents of growth and expansion, and that the polyps are only secondarily formed amongst and out of these. This is shown to be the case by a study of fig. 4; the growth at the edge of the colony is effected by the endodermic outgrowths (MOSELEY'S superficial layer of canals) which penetrate into the newly formed mesoglœa beneath the ectoderm, and thence grow outwards as new cœnenchyme cæca. (Compare p. 459.) An examination of the corallum at the growing edge, such as is represented in fig. 5, shows that new tubes originate as small triangular cavities, usually in the spaces where the walls common to three contiguous chambers unite together, and that they end blindly below. They are, in fact, intercalations between, and are not (with few exceptions), branches of pre-existing tubes.

Although in the absence of any positive evidence, such as would be afforded by a series of growing colonies from their first formation onwards, any attempt to explain the growth and formation of *Heliopora* must be open to correction, I believe that the following account is justified by a study of the architecture and mode of increase of the colony. In a flattened explanate frond there may be seen in vertical section a central core, composed, as I have already shown, of numerous polygonal tubes, having thin walls and a generally vertical ascending course. The colony being flat and

explanate, this central core might be described as an axial plane consisting of hollow tubes, arranged four deep, or thereabouts, and extending right through the frond, except at its extreme lateral edges. In horizontal section these central tubes show the same honeycomb structure as is exhibited at the growing edges of the fronds, and, indeed, the honeycomb work at these edges is nothing more than the extreme ends of the uppermost central tubes. In no case is the cavity of a calicle prolonged into the central system of tubes.

As the central tubes grow upwards, new tubes are constantly being formed and inserted amongst them; as we have seen they are inserted usually between three adjacent tubes.* Thus, in the course of growth, the number of tubes is constantly increasing, and in order that there may be room for the increasing numbers, some of the tubes are pushed over to one side, and that at such a sharp angle that they soon come to lie at right angles to the ascending central tubes. The external ends of the tubes after they have been deflected outwards become thickened by a secondary deposit of carbonate of lime within their cavities, as has already been described, and amongst them the calicles are formed, which are likewise set nearly perpendicularly to the central core; the inner ends of a few of them may bend downwards and reach the central tubes, without entering into them.

In the absence of very young specimens one can only guess at the first steps by which the colony was formed. I assume that it originates from a single mother polyp developed directly from the ovum. The polyp would be small, of inconsiderable height, and its lower moiety swollen by the presence of thickened mesoglœa. Into this thickened mesoglœa stolons in the form of endodermic diverticula from the cœlenteron, push their way, and these, branching and anastomosing amongst one another, give rise to vertically directed upgrowths, which are the first cœnenchymal cæca. These grow upwards pushing the ectoderm before them, and as growth proceeds, new mesoglœa is formed from the ectoderm, strings of calicoblasts pass inwards between and amongst the cœnenchymal cæca, and new cæca are formed by the ingrowth of endoderm cells into the newly-formed mesoglœa: the secretion of carbonate of lime by the calicoblasts leads to the formation of the calcareous cœnenchymal tubes (compare *supra*, p. 459).

A certain number of cœnenchymal cæca, probably a group adjacent to the mother polyp, which gets an abundant supply of nutriment, grow faster than the remainder, and as they grow new cæca are constantly being added among their upper extremities. The immediate result of this rapid growth with addition of new cæca is that the mother polyp is pushed to one side, and that at every stage a certain number of the cæca with their investing tubes are pushed to one side or the other to make room for the new ones that are constantly being added above. I have

* G. von Koch (10) p. 340, has correctly described this mode of increase of the cœnenchymal tubes; "Die Cönenchymröhrchen nicht durch Theilung sich vermehren, sondern die neuen . . . selbständig zwischen den älteren ihren Anfang nehmen."

attempted to represent this mode of growth in the diagram, fig. 10, which would serve as well as a truthful but diagrammatic representation of an actual vertical section through a frond of *Heliopora*. The flattened fronds characteristic of the great majority of the specimens of this genus seem to be due to the linear extension of the first formed tubes in a direction perpendicular to the surface of the paper in fig. 10. If such an extension takes place it is obvious that the older tubes cannot be pushed aside radially in all directions by the addition of new tubes amongst their upper extremities, but must be pushed either to the right or to the left where room can be found for them. The variety *Tuberosa* of Dana is formed when there is no such linear expansion of the newly-formed colony, and the tubes are free to radiate in all directions.

The colony of *Heliolites*, in section, shows a remarkable general correspondence with that of *Heliopora*. Its mass, however, differs in shape, being generally hemispherical or spheroidal, more rarely ramose or lobate. Examination of a section shows that there is a difference in the mode of growth which may account for the different form of the colony. In *Heliopora*, as has been shown, the tubes rarely branch, the rule being that new tubes are intercalated among the old and have no opening into the latter below. In *Heliolites* the tubes themselves branch dichotomously, and thus their increased number at the periphery is effected by a different method to that in *Heliopora* (see also VON KOCH (10), p. 334). The regular arrangement and more or less hexagonal shape of the tubes in *Heliolites* is probably due to this mode of growth. In *Heliopora* the intercalation of new tubes among the old which are, as we have seen, at first triangular in section and only subsequently become polygonal as they get more room for expansion, necessarily destroys the primitive symmetry of the tubes; I have not been able to follow out exactly the law of growth and symmetry, but it is clear that the asymmetrical arrangement is due to this cause.

A consideration of the mode of growth of *Heliopora* explains several features in the corallum. After the tubes have been pushed away from the vertical and have assumed a more or less horizontal position, they are closely packed together and there is no room left for the intercalation of new tubes between their outer ends. Further growth consequently ceases in the lateral parts of the colony, and the activity of the calicoblasts is limited to the formation of secondary deposits within the cavities of the tubes, and to the formation of the characteristic echinulations at the points where the walls of adjacent tubes unite.

A close study of the structure and mode of formation of the hard parts of *Heliopora* is of importance, since it is only by comparison of the hard parts of extinct corals that we are able to form any idea as to their affinities. The multiplication of the tubes (or corallites) by the intercalation of new tubes between the distal ends of those already existing, is characteristic of many of the so-called Tabulate corals. Such a mode of growth is well seen in many of the Favositidæ, *e.g.*, in *Favosites Forbesi* and

Bowerbankii. (Compare NICHOLSON (16), Plate 2, figs. 1A and 2B; Plate 3, fig. 4B.) It is particularly well marked in *Heteropora* (*vide* NICHOLSON 17, page 69, woodcut fig. 9C) in which the ascending vertical tubes, bending outwards to take a horizontal direction, are very similar to those in *Heliopora*, and the horizontal portions of the tubes are similarly thickened by secondary calcareous deposits. An equally striking superficial resemblance is to be seen in *Stenopora Jackii.* (*Vide* NICHOLSON 17, p. 81, woodcut fig. 10B and C.) It is clear, however, that the habit of growth is not to be relied upon as an indication of zoological affinity. In *Stenopora* the corallites would seem to be separate and independent of one another: each has its own proper wall, which is not even fused with the walls of adjoining corallites. In *Heliopora*, as we have seen, the walls of each tube are not even originally distinct, but are common to it and to adjacent tubes. I must insist here upon the fact, which has been abundantly proved in the course of this paper, and was originally pointed out by MOSELEY, that the walls of each tube are composed of several pieces, each of which takes a share in forming the walls of other tubes, and similarly the walls of the calicles are formed by numerous separate pieces, each of which takes a share in forming the walls of contiguous tubes. There is no fusion or amalgamation of separate tubes, corallites or calicles. This important fact has been entirely overlooked by NICHOLSON (16), who says, in describing the skeleton of *Heliolites*, which in this respect is similar to that of *Heliopora* (*loc. cit.* p. 244), "the corallites are universally and throughout in complete contact, their walls being so entirely amalgamated that no trace of their originally duplex constitution can be detected." This "duplex constitution" of the walls is a pure assumption, and, moreover, it is made in defiance of the ascertained structure of *Heliopora*, whose tube walls certainly have no such duplex constitution. Throughout his writings, NICHOLSON falls into this same error of assuming that wherever the walls of the corallites or cœnenchymal tubes of an extinct coral are not obviously separate from one another, they must nevertheless have been originally distinct and have been subsequently fused together. From my own observations, and from a comparison of the writings of other observers, it seems to me that the tabulate Alcyonarian corals may be divided into two distinct groups, according to the characters of their skeletons. In the one group each corallite, and, if they are present, each cœnenchymal tube also has its own distinct and proper wall, and if the corallites are closely apposed, so that their walls become contiguous, this primitive distinction is not lost. Such forms are represented in the present day by *Tubipora*, the characters of which genus have been amply described by VON KOCH (9) and HICKSON (4). I propose to call this group the *Autothecalia.*

In the second group the walls of the calicles and cœnenchymal tubes are not separate and independent, but the pieces forming the wall of each take a share in forming the walls of contiguous tubes or calicles. This group, for which I propose the name of Cœnothecalia, is represented in the present day by *Heliopora*, and among extinct forms by the closely allied *Heliolites*, by *Plasmopora*, *Propora*, and *Lyellia*,

and by the family of the Thecidæ, comprising the single genus *Thecia*. These forms have many features in common, and have been placed among or near the Helioporidæ by all recent observers. Whether *Halysites* and *Tetradium* are to be classed among the Cœnothecalia must remain doubtful for the present. *Tetradium minus* resembles *Heliolites* in the close approximation of its corallites, in the possession of tabulæ, and in the presence of pseudosepta. NICHOLSON and ETHERIDGE have been unable to decide whether the walls of the contiguous corallites are double or not. So far as I am able to judge, the balance of evidence is in favour of the walls separating adjacent corallites being single, and if this is the case, *Tetradium* must be ranked among the Cœnothecalia. It differs, however, from the Helioporidæ, in not having cœnenchymal tubes, distinct from and smaller than the calicles.

The evidence which leads me to think that *Halysites* must be included among the Cœnothecalia is contained in NICHOLSON'S account of the structure of the corallum (16, p. 227): "Every corallite in the corallum, except those which form the actual circumference, is united along its whole length, along opposite sides, to two other corallites, those which form the centre of three of the constituent laminæ of the mass being similarly united to three of their neighbours. This union is, moreover, not one of mere contact, but is absolute, the epitheca and wall of any given tube being directly continuous with the corresponding structures in the tubes which stand to the right and left of it." There are, however, considerable difficulties in understanding the manner in which the hard parts in *Halysites* can have been formed, and as I have not had the opportunity of making sections of this form, I must leave the question of its affinities an open one. I will only remark here that the structure described by NICHOLSON as "epitheca" cannot possibly be homologous with the epitheca of a Madreporarian coral; and from a study of his figures I am inclined to the belief that NICHOLSON'S epitheca may prove to be nothing more than an incrustation, the more so as it is described by him as being darker than the internal parts, and my experience of recent corals is that incrustations, generally of calcareous algæ, appear darker in section than in the true corallum. The presence of cœnenchymal tubes in *Halysites catenularia* must be taken as evidence in favour of its affinities with the Helioporidæ.

The Chætetidæ, which are said to have the walls of contiguous corallites completely amalgamated, must certainly be included among the Cœnothecalia, and they seem to be closely allied to *Tetradium*, the presence of the pseudosepta in the latter genus being, as MOSELEY has suggested, of secondary importance. Both *Tetradium* and *Chætetes* agree with one another, and differ from the Helioporidæ in the absence of cœnenchymal tubes.

As regards the Monticuliporidæ, I believe that NICHOLSON is perfectly right in regarding them as allies of the Helioporidæ. But if, as he supposes, the corallites of all the Monticuliporidæ were primitively distinct, and have only become secondarily amalgamated together in such forms as *Monticulipora petropolitana* and *M. undulata*,

whilst their primitive distinctness is preserved in *M. pulchella*, *M. petasiformis*, and *M. Andrewsii*, they would have to be removed from the Cœnothecalia and placed among the Autothecalia, that is to say, they would be allies of *Tubipora* rather than of *Heliopora*. But I am not satisfied that there is any such primitive independence of the corallites in *Monticulipora*, as is described by NICHOLSON. As evidence of their independence he brings forward the structure of the corallum as shown in their sections, and the results obtained by rough fractures, which, he says, invariably expose the walls and not the interior of the tubes.

Passing over the fact that too much importance cannot be attached to results obtained by such a very crude method of investigation as that of rough fracture, I wish to point out that the cleavage of any coral which is roughly broken must correspond to the lines of least resistance, and will depend in each case rather on the mineralization of the specimen than on the original structure of its corallum. I have, for instance, before me a beautiful specimen of *Favosites gothlandica* from the Upper Silurian of N. America, which has been kindly lent me by Professor A. H. GREEN. The corallum shows the characteristic basaltiform structure, and the corallites are completely filled up with hard calcite. The original walls of the corallites are preserved, but have undergone partial disintegration, and are of soft and chalky consistency. This chalky substance can easily be scraped off with a knife, and is shown to be composed of numerous small prisms of calcium carbonate. The walls are so soft that they may be used for drawing on a board like a piece of chalk. When the coral is fractured, the hard prisms of calcite readily separate from one another, the lines of fracture following the soft walls of the corallites and transversely of the tabulæ. Each prism, when separated, is surrounded by the soft chalky matter which represents the old wall of the corallite, and it certainly looks as if the individual corallites had their own proper walls, which are only apparently fused by close contact. But it would be difficult to prove that the appearance of a distinct wall belonging to each corallite was not brought about by the adherence of the partially-disintegrated single walls of the corallites to the prisms of calcite as they are pulled away from one another. The evidence afforded by sections does not make the subject any clearer. Through Professor GREEN'S kindness I have been able to examine some very beautiful sections of *Favosites*. In these, the dark line running up the centre of the partition wall between two corallites is very well marked, but a similar dark line is equally well marked in the centre of each tabula. If the dark line in the partition walls is evidence of their being composed of two closely-apposed plates, it must equally be held to be evidence of each tabula being composed of two superimposed plates. From what we know of the formation of tabulæ in recent forms—they are formed in periods of quiescence alternating with periods of growth by the activity of the calicoblasts at the basal blind ends of the polyps or cœnenchymal cæca—there are grave difficulties in the way of accepting such an explanation. On the other hand, students of recent corals are well acquainted with dark central lines

M. trentonensis, which indicate the steps by which the condition of *M. Girvanensis* may have been arrived at.

Should my views prove to be correct, there can be no doubt that the Monticuliporidæ would stand in close relationship with the Helioporidæ, which they resemble in general structure and mode of growth, in the presence of tabulæ, and in the presence of larger polyp cavities and smaller cœnenchymal tubes. Should the contrary prove to be the case, the Monticuliporidæ must be removed from the Helioporidæ and placed near to the Tubiporidæ and their allies.

It is proper here to enter into the question of the nature of the cœnenchymal cæca in *Heliopora*. They were compared by MOSELEY to the siphonozooids of *Sarcophyton*, and it has been assumed, by many subsequent writers, that the presence of cœnenchymal tubes in any tabulate coral is evidence of those corals being dimorphic and having two distinct kinds of polyp, autozooids and siphonozooids. VON KOCH, however, had expressed a doubt as to MOSELEY'S interpretation of the cœnenchymal tubes of *Heliopora*. In this matter I must agree with VON KOCH. The cœnenchymal tubes of *Heliopora* appear to me to be nothing more than specialised portions of a system of tubular off-sets of the polyp cavity. The fact that they have no opening to the exterior and that they show no trace of mesenteries, stomodæum or tentacles, might be explained, as MOSELEY explained it, by the extreme degeneration of the siphonozooids which he supposed them to represent. But in the case of a truly dimorphic Alcyonarian, such as *Sarcophyton*, each siphonozooid is a reduced autozooid and resembles it in essential structure; if an autozooid were formed from a siphonozooid, it would be by the complete development of the tentacles, stomodæum and mesenteries of the latter, and not by the coalescence of several siphonozooids.

In *Heliopora*, we do not find that a single cœnenchymal cæcum undergoes complete development to form a polyp, but that a group of cœnenchymal cæca is arrested in development, and that a calicle takes the place of some seven central cœnenchymal tubes, and that twelve or more immediately circumjacent tubes enter into its composition. In other words, the autozooid is the result of the arrest in growth of a group of supposed siphonozooids, a process which is not known to occur in any Alcyonarian in which true siphonozooids are undoubtedly present. The calicle in *Heliopora* is not, as has been shown, autonomous, but is formed by the walls of adjacent cœnenchymal tubes, whereas in any dimorphic Alcyonarian, the walls of each autozooid are proper to itself, and adjacent siphonozooids take no share in their composition. The case of *Xenia* and *Heteroxenia* to which I shall refer later on, throws some light on this point. In the genus *Xenia* there are no true siphonozooids, but some of the polyps may remain for a long time arrested in development. Eventually, most of these arrested polyps grow directly into fully formed polyps, but whether they are arrested or fully developed, their cavities are always distinct and separate, and communicate with those of adjacent polyps, only by means of endodermic canals. In *Heteroxenia* there are true siphonozooids, which are sterile, whilst the

running through sections of coralla—"dark lines of growth," as they are usually called. Without venturing on any positive assertion in the case of *Favosites*, I would point out that conclusions drawn from the existence of central dark lines and from rough fractures must be received with caution.*

To return to the Monticuliporidæ. In *M. petropolitana* and *M. undulata* a tangential section of the corallum exhibits the partition walls as thin dark lines (17, figs. 1A and 2A, pp. 37 and 38). There is no trace, as NICHOLSON admits, of any division in the partition walls in these species. In a similar section of *M. pulchella* dark central lines may be seen in each partition wall, thickening to form nodal points where the walls unite with one another. The structure exhibited in *M. petropolitana* and *undulata* may be compared with my figure of the newly-formed skeleton in *Heliopora;* that exhibited by *M. pulchella* may be compared with my figure of a section of the fully-formed skeleton in *Heliopora.*

In the last-named figure, "the visceral chamber of each corallite is seen to be surrounded by its own investment of light-coloured sclerenchyma, and to be separated from the corresponding investment of all the tubes in immediate contiguity to it by a clearly marked (dark) line, which is often thickened into larger or smaller nodes at the angles of junction of the corallites." The sentence in inverted commas is NICHOLSON'S description of a section of *Monticulipora pulchella,* and it would nearly describe the section shown in fig. 8.

Under a somewhat lower power, the correspondence of the description with the section would be even more striking. I do not wish to press the point too closely, as a further examination of the Monticuliporidæ would be necessary before any definite conclusion could be arrived at, but I would suggest that NICHOLSON'S light-coloured sclerenchyma is analogous, if not homologous, to the secondary deposits in the calicles and cœnenchymal tubes of *Heliopora,* and the dark central lines are the expression of the primary constituents of the skeleton, comparable in all respects to the skeletal tissue shown in fig. 7. If this were so, *Monticulipora petropolitana* and *M. undulata* would stand in the same relation to *M. pulchella,* as *Heliolites,* the walls of whose cœnenchymal tubes and calicles are not thickened by secondary deposits, stands to *Heliopora.*

The structure of *M. Girvanensis,* whose corallites certainly seem to be distinct, and almost disjunct, may be held to prove the contrary of my assumption, but the structure of this species may be explained by reference to *M. implicata* and

* Since writing the above I have come across a sentence of G. VON KOCH'S (10) which bears directly upon the question. In describing the structure of *Favosites,* he says (p. 343), "Die Mauerblätter liegen nämlich dicht aneinander so dass zwischen ihnen nur auf Schliffen Trennungslinien wahrnehmbar sind"; and he adds in a footnote, "Vielleicht sind diese auch die primären Anlagen der Mauerblätter, welche erst secundär verdicken." I have given reasons for thinking that the corallites of *Favosites* are really distinct, but the opinion of VON KOCH, who is one of the greatest living authorities on the structure of corals, and has specially studied them by means of sections, must be held as adding great weight to the opinion which I have expressed as to the structure of the corallites of the Monticuliporidæ.

autozooids are fertile. The siphonozooid cavities penetrate but a short way into the cœnenchyme, and give rise to numerous endodermic canals which place them in communication with the polyp cavities. Each siphonozooid is, however, a distinct individual, with its own proper walls, and there is no evidence of the polyps or autozooids being formed by the coalescence of several siphonozooids, but rather that the last named are simply arrested and modified autozooids.

To find a parallel to the cœnenchymal tubes in *Heliopora* we must go outside the Alcyonaria and make a comparison with the Milleporidæ. In *Millepora* the external surface of the colony is covered in, much as it is in *Heliopora*, by a continuous sheet of ectoderm, of which the continuity is broken here and there by the mouths of the autozooids. The superficial ectoderm is continuous with the ectoderm covering the exsert moieties of the autozooids and dactylozooids. Beneath the superficial ectoderm and connecting the autozooids and dactylozooids with one another is a ramifying canal system, the most superficial branches of which take a direction perpendicular to the surface (*vide* MOSELEY (15), Plate 3, fig. 10). These canals are not in any way comparable to degenerate zooids, but are described, no doubt correctly, by MOSELEY as a hydrophyton consisting of inosculate canals, separated from one another by the calcareous trabeculæ which take the place of the chitinous perisarc in such allied forms as *Hydractinia* and *Podocoryne*. Without asserting any homology, I wish to point out that physiologically the cœnenchymal tubes of *Heliopora* are strictly comparable to the inosculating canals of the hydrophyton of *Millepora*, and that the relations of both to the superficial ectoderm and to the skeleton are remarkably similar. By adapting ALLMAN'S exact terminology to the Anthozoa, one might legitimately describe the cœnenchymal tubes of *Heliopora* as an Anthophyton, consisting of a system of adjacent tubes united by an interosculating network of canals, amongst which are calicular excavations into which the zooids, which are formed as specialised buds from the canals, are retracted. If anyone will compare my figure of the soft tissues of *Heliopora* with MOSELEY'S figure of the structure of *Sarcophyton* (14), and with his figure of the structure of *Millepora* (15), I think they will agree with me that the conclusion that the cœnenchymal cæca of *Heliopora* are not of the nature of degenerate siphonozooids is a just one.

Finally, there is the relationship of *Heliopora* with the Favositidæ to be considered. MOSELEY was inclined to place the Favositidæ very close to the Helioporidæ, for reasons which certainly carry much weight. But whilst I am completely satisfied as to the position of the Favositidæ amongst the Alcyonaria (there is really not a shadow of evidence in favour of placing them with NICHOLSON among the perforate Madreporarians), I am inclined to classify them among the Autothecalia rather than among the Cœnothecalia. Although I have referred above to the doubtful nature of the evidence afforded by sections and rough fractures in the case of *Favosites Gothlandica*, I do not mean to assert that in this and other Favositidæ the corallites are not distinct, but merely to show that their independent nature cannot be

asserted on this evidence alone. The appearances obtained by sections and fractures of *Favosites* may be interpreted in favour of the distinct nature of their corallites, and that they really are distinct is, I think, rendered extremely probable by the comparison of *Stenopora*, *Syringopora*, and *Syringolites*. In *Stenopora*, which is undoubtedly a member of the Favositidæ (*vide* NICHOLSON, *loc. cit.*, pp. 168–177), the carollites would appear to be separate and distinct from one another, though even here it would be difficult to say that the appearances are not due to the thickened secondary deposits having almost entirely taken the place of the first formed prismatic constituents of the skeleton. But in the case of *Syringopora* and *Syringolites* there can, I think, be no doubt. *Syringopora* has widely separated corallites, and HICKSON (4) has shown very good reasons for placing it very close to *Syringolites*, the coincidence between the form of the tabulæ being very striking. On the other hand, *Syringolites* is obviously closely related to the Favositidæ, and thus there is a connection between a form with separate individual corallites, *Syringopora*, and one with closely adherent corallites, *Favosites*. The other evidence afforded by sections and fractures, and the existence of mural pores which are undoubtedly homologous with the connecting processes in *Syringopora* and the canals of the platforms in *Tubipora*, leave no doubt that the Favositidæ must be classed as Autothecalia, and must therefore be removed from the Helioporidæ. As to the Columnariadæ, there can be no doubt, since in some forms, *e.g.*, *Columnaria calicina*, NICH., the corallites are disjunct. It is possible, however, that this form and its allies belong to the Madreporaria. The septa of *C. calicina* as figured by NICHOLSON (16, p. 198, fig. 28, 1*b*), are arranged in two cycles of 14, making 28 in all, a larger septum of one cycle alternating with a smaller septum of the other. Such an arrangement is unknown in any Alcyonarian, and suggests decided affinities with the Madreporaria. To sum up, I suggest the division of the tabulate Alcyonarians into two groups, the Autothecalia and the Cœnothecalia. In the former group I place the recent form *Tubipora* and its extinct ally *Syringopora*. It is exceedingly probable that *Syringolites* and the Favositidæ belong to this group, and the Columnariadæ may be provisionally placed in it. The Cœnothecalia are represented in the present day by *Heliopora*, and extinct forms undoubtedly belonging to the group are *Heliolites*, *Thecia*, *Plasmopora*, *Propora*, and *Lyellia*. *Tetradium* and *Halysites* are probably members of the same group. The Chætetidæ must certainly be ranked among the Cœnothecalia, in spite of the absence of cœnenchymal tubes, and the Monticuliporidæ may be provisionally placed in this group, though further examination may lead to the conclusion that the walls of their corallites are really distinct, in which case they would belong to the Autothecalia.

I have shown, as I think, conclusively, in the earlier part of this paper, that the skeleton of *Heliopora* is ectodermic. A chance examination of some members of the Xeniidæ has shown me that the spicular skeleton of other Alcyonarians may be entirely ectodermic.

The Xeniidæ are well known to have a skeleton composed of minute calcareous discs, compared by KÖLLIKER (11) to blood-corpuscles, which in some species they resemble in form and size. The family has been divided into two genera, *Xenia*, in which the colonies consist of one kind of polyp only, and *Heteroxenia* in which the colonies are dimorphic, consisting of autozooids, surrounded by more numerous imperfect siphonozooids. Recently WRIGHT and STUDER (20) have rejected the genus *Heteroxenia*, on evidence given by W. HAACKE (3), who observed the growth of living Xeniidæ in the Torres Straits.

I shall show later, that KÖLLIKER'S genus is apparently good, and that HAACKE'S criticisms must have been founded on a study of members of the genus *Xenia*, which we know from SAVILLE KENT'S recent work to be abundant in the Torres Straits and on the Great Barrier Reef of Australia.

My specimens consist of two species of *Xenia*, collected by me at Diego Garcia, in 1886, and a fine colony of *Heteroxenia*, brought by Dr. GULLIVER from Zanzibar, and placed in the Linacre Department of the Oxford University Museum. The specific characters of the Xeniidæ have been very imperfectly defined, and the figures illustrating the different species leave very much to be desired, exception being made in both respects of KLUNZINGER'S work (7). Hence, I have had some difficulty in identifying the specimens in my possession.

Genus *Xenia*, SAVIGNY.

Xenia umbellata, SAV. (Apud. 'Lam.,' ed. ii., p. 625).—BLAINVILLE, 'Actinol.,' p. 523, SCHWEIGGER, 'Beob. auf Reisen,' tab. 5, figs. 48–50, EHRB. 'Korallen,' p. 53, DANA, 'Zooph.,' p. 604, M. EDW. and HAIME, 'Cor.,' tom. 1, p. 125, KÖLLIKER, 'Icon. Hist.,' p. 133, and 'Festschrift der Physikal.-Medicin. Gesell. in Würzburg,' 1874, p. 17, GRAY, 'Ann. Mag. Nat. Hist.,' 1869, p. 126, HÆCKEL, 'Arab. Kor.,' p. 44, tab. 1, fig. 8, KLUNZINGER, 'Kor. Roth. Meeres,' part 1, p. 39 (figs. 11, 11*a*, and 12).

One of the specimens which I brought from Diego Garcia is undoubtedly referable to this species. It belongs, however, to the variety *Cærulea*, described as separate species by EHRENBERG, *vide* KLUNZINGER, *loc. cit.*, p. 41. The characters of the variety are those of the species, but the dimensions are in all respects smaller. In my specimens, preserved in spirit, these are: length of polyp, with tentacles, 5·25 millims., length of tentacles, 2·7 millims., breadth of polyp, 0·8 to 1 millim., length of pinnæ, 0·4 millim., breadth of pinnæ, 0·1 millim. The pinnæ are arranged in three alternate rows on each side of the tentacles, and are slender and filiform. The stomodæum is short, the spicules numerous, minute flattened discs, about 0·02 millim. in greatest diameter, and 0·005 millim. in thickness, forming an investment in the deeper parts of the ectoderm, closely applied to the mesoglœa.

Xenia Garciæ, n. sp., Plate 12, figs. 13 and 14.—An encrusting base from which spring stout, short, fleshy branches, which are longer and more distinct than in

X. umbellata. The summits of the branches bear numerous polyps, less crowded together than in *X. umbellata*, with shorter and stouter tentacles, pinnæ short, and digitiform arranged in three closely apposed alternate rows on the sides of the tentacles. Numerous imperfect polyps or buds in all stages of growth at the edges of the polyp-bearing summits; these are not siphonozooids but stunted or developing polyps. Spicules numerous, irregular, or ovoid in shape, minute, varying from ·02 to ·01 millim. in greatest diameter; rounded and not discoid like those of *X. umbellata;* in the exsert part of the polyps the spicules are situated in the ectoderm, in the stem and branches the spicules are embedded in the mesoglœa, which is penetrated by strands of ectoderm, from the cells of which the spicules are developed. Around each polyp cavity there is a ring of mesoglœa free from spicules. Length of polyp and tentacles 5 millims., length of tentacle, 2 millims., length of pinnæ, 0·4 to 0·5 millim., breadth of pinnæ, 0·2 millim., breadth of polyp, 0·9 millim.

Habitat.—Diego Garcia, in the Indian Ocean.

I have been unable to refer this form to any described species. In size and habit it much resembles *X. umbellata* var. *cærulea*, but differs from it in the size and stoutness of the pinnæ (compare figs. 11*a* and 14), in the shape of the spicules, and in the relations of these to the mesoglœa. The specimens are described in my diary as a pretty lilac-coloured fleshy Alcyonarian, having a brown streak on the inner surface of each tentacle, from which a branch is given off to each pinnule. When alive it secreted a quantity of mucus in which were a number of highly refracting oval bodies, but I failed to determine that these were nematocysts even under high powers of the microscope. The brown streaks on the tentacles and pinnæ were due to a number of small roundish yellow granules, which I suspected to be Zooxanthellæ, but having no chemicals with me, I was unable to test them for starch.

Genus *Heteroxenia*, Kölliker.

Heteroxenia Elizabethæ, Kölliker. 'Festschrift der Physik.-Medicin. Gesellsch. in Würzburg,' 1874, pp. 12–17, Table 2, figs. 7 and 8.

I have been unable to procure a copy of Kölliker's work, and must, therefore, refer the Zanzibar specimen in my possession provisionally to this species. The specimen agrees with Klunzinger's figures and description of *Xenia fuscescens*, Ehrb., of which he says that it is very similar to *Heteroxenia Elizabethæ*, Köllik., but that the dimensions of the latter are much greater.

I have given, in fig. 15, a drawing of my specimen, the actual dimensions of which are, height of stem, 25 millims.; breadth of stem below polyps, 10 millims.; length of body of larger polyps, 10 millims.; length of tentacles, 4·5 to 5 millims.; breadth of polyp, 2 millims.

The polyps, which are of two kinds, are borne on the distal flattened or umbellate expansion of an erect sparingly branched fleshy stem. The larger polyps have well

developed tentacles, with three lateral rows of alternate pinnæ on their margins; their cavities are continued to the bottom of the stem, or nearly so, and they are sexual, all my specimens being filled with ova. Amongst the larger polyps are more numerous closely apposed smaller sterile zooids, which have no tentacles, but only eight radiate lobes surrounding the mouth. They have short polyp cavities extending but a little way into the fleshy stem, and communicating with the cavities of the larger zooids by anastomosing endodermic canals. At the edges of the umbellate expansion there are numerous young polyps in all stages of development, many of which show distinct pinnate tentacles, but there are never, among the smaller zooids on the summit of the expansion, any individuals which show signs of developing tentacles, nor have I been able in any case to find sexual products in their shortened polyp cavities. There can be no doubt that in this form there is a distinct dimorphism; the colony consists of large tentacle-bearing fertile autozooids, and smaller sterile siphonozooids with very rudimentary tentacles. The spicules (fig. 15A) are minute, fairly numerous in the exsert bodies of the autozooids and in their tentacles, less numerous in the siphonozooids, and few in number in the stem. They are flattened, rarely discoid, more generally of a figure of eight shape, about 0·02 millim. in their longest diameter by 0·01 millim. in their lesser diameter, and 0·0075 millim. in thickness. HICKSON (5) has pointed out that in the siphonozooids of *Heteroxenia* there is a well developed "siphonoglyphe," which is absent in the autozooids.

The present interest in these forms lies in the nature and position of the skeleton. The spicules, which are sufficiently well described above and are shown in figs. 12, 13, and 15*a*, are somewhat feebly calcareous, and contain an abundant organic basis which causes them to stain readily in hæmatoxylin. Fig. 16 is a represention of a transverse section across the stem of *Xenia umbellata*, at some distance below the polyp-bearing summit. In the upper part of the figure an isolated polyp has been cut across, and a few deeply stained scattered spicules are seen in its ectoderm. They clearly lie wholly outside of the mesoglœa. The same is seen to be the case at the edge of the section through the stem. Here there is a continuous layer of ectoderm covering the stem, and in it are numerous spicules, which clearly are embedded in the ectoderm, and are not contained in the mesoglœa. The section has cut through six polyp cavities and portions of two others. Each cavity is seen to be surrounded by a definite ring of structureless mesoglœa, in which there is no trace of cells or of spicules.

The mesoglœal rings surrounding the polyps are connected one with another by mesoglœal strands, and here and there endodermic canals (*ed. c.*) are seen in section, each surrounded by a mesoglœal sheath. The spaces between these structures are occupied by a tolerably abundant "cœnenchyme," which is filled with numerous spicules. This cœnenchyme is composed of cells which exactly resemble those of the external ectoderm, and a direct continuity between the cœnenchyme and the ectoderm is traceable in many places when study is made of a series of transverse

sections. This "cœnenchyme," as may be seen in the section, is not of the nature of a mesoglœa which has been invaded by ectoderm cells, but is rather the fused ectoderm of closely adjacent polyps, which are also united by a few endodermic canals, which put their cavities into communication, and by strands of mesoglœa, which hold the polyps more firmly together. The section is sufficient evidence of the wholly ectodermic character of the spicules.

In longitudinal sections the continuity of the ectoderm of the exsert moieties of the polyps with the "cœnenchyme," which occupies the spaces between their insert moieties, is very well seen.

In *Xenia Garciæ* (fig. 17) the ectoderm of the exsert portions of the polyps is crowded, as in *X. umbellata*, with spicules, which almost fill up its entire thickness in the tentacles and pinnæ. The mesoglœal lamina is thicker than in *X. umbellata*, and in the stem the thickened mesoglœa of the insert moieties of the polyps appears in section as a broad structureless band surrounding each polyp cavity. The polyps are closely crowded together in this region, and their mesoglœal laminæ may either be separated by a thin spicule-bearing layer of ectoderm, or may be confluent, in which case the thickened mesoglœal cœnenchyme resulting from their union is penetrated by strands of ectodermal tissue in which spicules are more or less abundantly developed. Endodermic canals, by which the cavities of adjacent polyps are placed in communication with one another, are more numerous than in *X. umbellata*, and there is a special superficial system of these canals (*sp. c.*) lying close beneath the external ectoderm, which is interrupted here and there by the ingrowths of the ectoderm, which pass in and among the polyps.

In *Heteroxenia Elizabethæ* (fig. 18) there is a further advance towards the condition characteristic of *Alcyonium* and other forms. The structure of the exsert portions of both autozooids and siphonozooids is similar to that of the same parts in *Xenia umbellata* and *X. Garciæ*. The cavities of the siphonozooids do not reach far down into the stem, but open after a short course into numerous inosculating endodermic canals, which connect them with the cavities of the autozooids. Below the point where the siphonozooid cavities die out, the autozooid cavities, which are continued down to the base of the stem, are imbedded in a thick homogeneous mesoglœa, in which the primitive separation of the mesoglœal laminæ of the individual polyps is scarcely recognisable. This mesoglœa is permeated by endodermic canals, which become less numerous in the deeper parts of the stem, and there is, as in *X. Garciæ*, a special set of superficial canals lying close beneath the ectoderm. Ectodermic ingrowths pass in between the superficial canals and give rise to strands of cells which run everywhere in the mesoglœa between the polyp cavities, but do not invade the mesoglœal layer immediately surrounding them, so that in section each appears to be bounded by a homogeneous structureless ring, which is nevertheless continuous with and not distinguishable from the mesoglœa which the ectodermic ingrowths have invaded.

Thus in three species there are displayed successive grades of differentiation in the union of a bunch of polyps to form a colony, and in the cœnenchyme which binds them together and forms the common stem by which their proximal portions are united. These forms are of interest as indicating how the steps by which skeletal structures, which are at first purely ectodermic, may, as a consequence of the great thickening and subsequent fusion of the mesoglœa of contiguous polyps, lose their primitive position and become wholly included, as are the spicules of *Alcyonium* and the majority of the Alcyonaria, in the mesoglœa. The spicules of all Alcyonaria have long been known to be developed in cells which primitively belong to the ectoderm, but subsequently lose their connection with it, invade the mesoglœa, and give rise to the skeleton, whilst no spicules are found in the definitive ectoderm after the separation of the skeletogenous cells. In *Xenia umbellata*, however, we have a form in which the spicules are formed *in situ* in the ectoderm, and the cœnenchyme is not formed by the confluent much-thickened mesoglœa of contiguous polyps, but by the ectoderm of the confluent basal parts of a bunch of polyps.

The structure of *Xenia umbellata* is also eminently suggestive of the mode in which the skeleton of *Heliopora*, described in the earlier part of this paper as ectodermic, may have been phylogenetically developed. It has been shown that the mesoglœa and the calicoblasts of *Heliopora* are formed *pari passu* at the expense of cells proliferated from the ectoderm. In the three species, *Xenia umbellata*, *X. Garciæ*, and *Heteroxenia Elizabethæ*, we find in the first named a purely ectodermic skeleton; in the second, a stage in which the mesoglœa is being thickened and added to at the expense probably of those ectodermic cells which do not give rise to spicules, and, at the same time, a differentiation in the endodermic canal system. In the third, the thick homogeneous mesoglœa is formed by numerous cells proliferated from the ectoderm amongst which a few give rise to spicules. The evolution of *Heliopora* seems to have followed analogous though somewhat different lines. The calcigenous cells, the calicoblasts, have been greatly increased at the expense of those which form the mesoglœa, consequently the cœnenchyme is not mesoglœal, with a small admixture of ectodermic skeletal elements, as in Alcyonium, but is chiefly composed of ectodermic skeleton, the mesoglœal constituents having sunk to a quite subordinate position The differentiation of the superficial canals in *Xenia Garciæ* and *Heteroxenia Elizabethæ*, from which the new buds are formed at the edges of the umbellate expansion, also suggest the steps by which the complicated system of cœnenchymal tubes and their connecting network may have been arrived at in *Heliopora*. In both cases a superficial set of endodermic canals is formed, from which new polyps take their origin as buds. I do not wish to suggest that the Helioporidæ are derived from the Xeniidæ, but it is likely enough that both are derived from a common ancestor, in which the skeleton was completely ectodermic, and that differentiation has been effected, in the case of the Helioporidæ by the specialisation of the endodermic canals and the extreme

development of the calcigenous elements, in the case of the Xeniidæ, by the development of a thick mesoglœal cœnenchyme at the expense of the calcigenous elements, and a subordinate but, on the whole, well marked differentiation of the endodermic canals.

Finally, I may point out how much the progressive development of the mesoglœa in the Xeniidæ, accompanied by intrusion of ectodermic elements, which were originally distinct from it, bears out the views as to the nature of the mesoglœa which I expressed in my paper on the Anatomy of the Madreporarian Coral *Fungia* (1).

In conclusion, I may add that the whole of my work was carried on in the Linacre Department of Comparative Anatomy at Oxford, and I need hardly say how much I am indebted to Professor RAY LANKESTER, to whom I owe many thanks for advice and assistance, as well as for the specimens of *Heliopora* and *Heteroxenia*, without which I should have been unable to prosecute my studies.

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Description of Plates. 10–13.

PLATE 10.

Fig. 1. A single polyp with the adjacent soft tissues of *Heliopora*, as seen after removal of the skeleton by decalcification. Partly diagrammatic. P^1., the exsert moiety of an expanded polyp, bearing eight pinnate tentacles. P^2., the proximal insert moiety of the same. *ec.*, the continuous sheet of ectoderm which clothes the whole surface of the colony. *sp.c.*, superficial canal system lying directly beneath the ectoderm. *ct.*, cœnenchymal cæca.

Fig. 2. Portion of a decalcified colony of *Heliopora cærulea* viewed from above. The superficial ectoderm has been stripped away exposing the superficial network of canals. Two retracted polyps are seen at *P.P.* in which it is obvious that there is no correspondence between the mesenteries and the pseudoseptal invaginations. The cœnenchymal cæca, *ct.*, are seen in optical section.

Fig. 3. Part of a vertical section through the soft tissues at the growing edge of a frond of *Heliopora*. The outlines are drawn in with a camera lucida; the details are filled in diagrammatically, the mesoglœa in dark line or shadow, the endoderm in light shadow. The discontinuous lines and dots represent the calicoblasts. *ec.*, superficial ectoderm. *ct.*, cœnenchymal cæca. *P.*, a polyp cavity. *mt.*, mesenteries.

Fig. 4. A portion of the above section more highly magnified. *ec.*, ectoderm. *mg.*, definite layer of mesoglœa in the wall of a cœnenchymal cæcum.

mg'., mesoglœa in process of formation from the ectoderm. *en.*, endoderm lining a cœnenchymal canal. *ed.c.*, outgrowths of endoderm into the newly-formed mesoglœa. *zx.*, zooxanthellæ. *div.*, diverticula of a cœnenchymal cæcum. *cal.*, calicoblasts.

Fig. 4A A group of proliferating ectoderm cells, highly magnified.

Fig. 5. Surface view of the hard tissues of the growing edge of a frond of *Heliopora*. ZEISS, A.A., Oc. 2.

PLATE 11.

Fig. 6. Surface view of a fully-grown portion of a colony of *Heliopora*, showing the calicles, with their pseudosepta, the cœnenchymal fenestræ, the superficial echinulations, and the shallow canals between them in which the superficial canals lie.

Fig. 7. Portion of a tangential section through the growing edge of the corallum of *Heliopora*. *b.b.*, point to the union of three calcareous lamellæ to form a triradiate figure. *a.a.*, point to the sutures connecting the arms of adjacent triradial figures.

Fig. 8. Portion of a section parallel to the surface of an older portion of a colony of *Heliopora*. *cy.*, calicle, around the diminished cavity of which is a thick secondary deposit. *ct.*, cœnenchymal tubes whose cavities are partially occluded by annular secondary deposits. Between them is seen the trabecular skeleton which was first formed at the growing edge of the frond. The dark lines round the cœnenchymal tubes in the lower part of the figure show the concentration of the blue colouring matter of the corallum in definite zones.

Fig. 9. Diagram illustrating the essential structure of the corallum in *Heliopora* and *Heliolites*. *C.T.*, cœnenchymal tubes, the walls of each of which are composed of 12 separate laminæ which take a share in the composition of the walls of six adjacent tubes. *a.a.*, *b.b.*, as in fig. 7. In the centre of the figure a calicular cavity is indicated, formed by the arrest, complete or partial, of a group of 19 cœnenchymal tubes, numbered I.–XIX. The outlines of the arrested tubes are shown by dotted lines. The pseudosepta, 1–12, are seen to be formed from the walls of the circumferential partially arrested tubes, viz., VIII.–XIX. To the left, the secondary deposits formed within the cœnenchymal tubes of *Heliopora* are indicated.

Fig. 10. Diagram illustrating the mode of growth and architecture of a colony of *Heliopora cærulea*. The arrangement shown in the diagram may easily be followed in a vertical section through a frond of *Heliopora cærulea*. *P'*, mother polyp, from which the colony has been developed. P^2, P^3, etc., daughter polyps successively formed among the cœnenchymal tubes. The centre of the colony is seen to consist of generally vertical ascending

tubes. As fresh tubes are added among their upper ends, they are successively pushed out of the vertical and come to take a horizontal position. In the diagram, the black lines represent the skeleton, the cavities are left white. *t.t.* tabulæ.

Fig. 11. A colony of *Xenia umbellata var. cærulea.* Natural size.

Fig. 11A. A tentacle of the same magnified, to show the pinnæ.

PLATE 12.

Fig. 12. Spicules of *Xenia umbellata.* ZEISS, D., Oc. 4.

Fig. 13. Spicules of *Xenia Garciæ.* ZEISS, D., Oc. 4.

Fig. 14. A group of polyps from a colony of *Xenia Garciæ,* magnified, to show the pinnæ.

Fig. 15. Drawing of a part of a colony of *Heteroxenia Elizabethæ,* which has been cut in half vertically. *Az.*, autozooids. *Sz.*, siphonozooids. *G.*, gonads in the cavities of the autozooids.

Fig. 15A. Spicules of *Heteroxenia Elizabethæ.* ZEISS, D., Oc. 4.

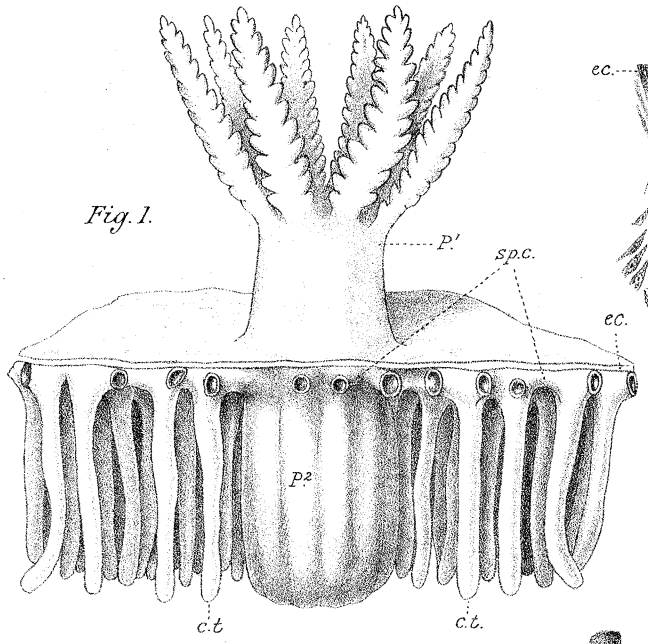
Fig. 16. Part of a transverse section through the stem of *Xenia umbellata.* *P.*, polyp cavities with mesenteries. *ec.*, ectoderm covering the surface of the colony. ec^2., ectoderm forming the cœnenchymal mass in which the polyp cavities are embedded. *ed. c.*, endodermic canals. *m.*, mesoglœa. ZEISS, B., Oc. 2. (In this and the two next figures, the general features are drawn in accurately with the camera lucida. The spicules which appear as dark spots, looking like nuclei, are shown in their proper proportion and situation, but the details of ectoderm and endoderm are filled in diagrammatically, the size of their cells being too small to be satisfactorily represented under the low magnification.)

PLATE 13.

Fig. 17. Part of a transverse section through the stem of *Xenia Garciæ.* *sp. c.*, superficial endodermic canals. The remainder of the lettering as in fig. 16.

Fig. 18. Part of a transverse section through the stem of *Heteroxenia Elizabethæ.* The polyp cavities are embedded in a mass of homogeneous mesoglœa, which is penetrated by numerous strands of ectodermic tissue some of the cells of which develop spicules. Lettering as before.

Fig. 1.



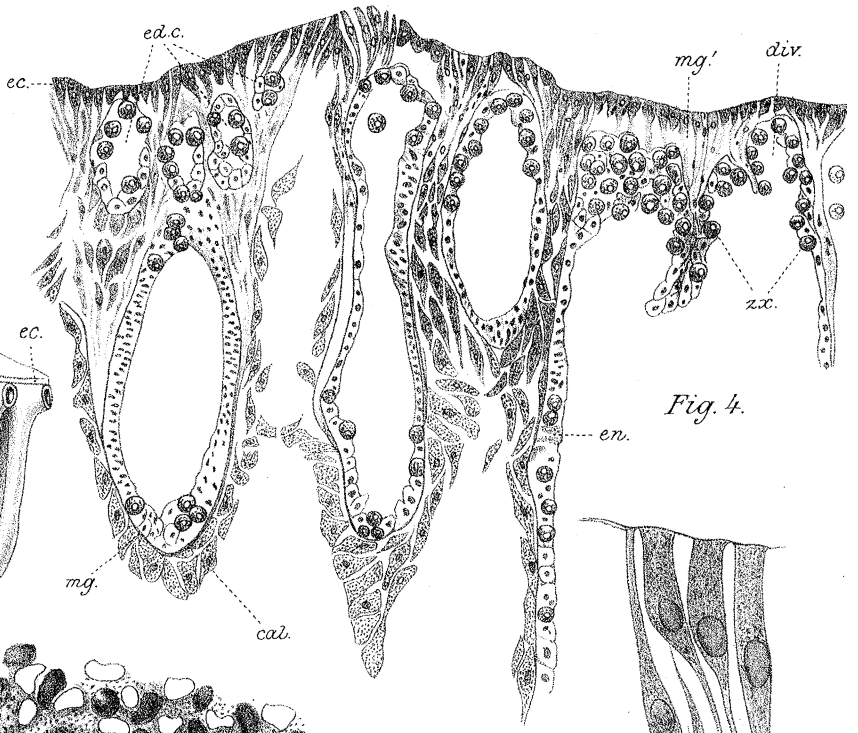
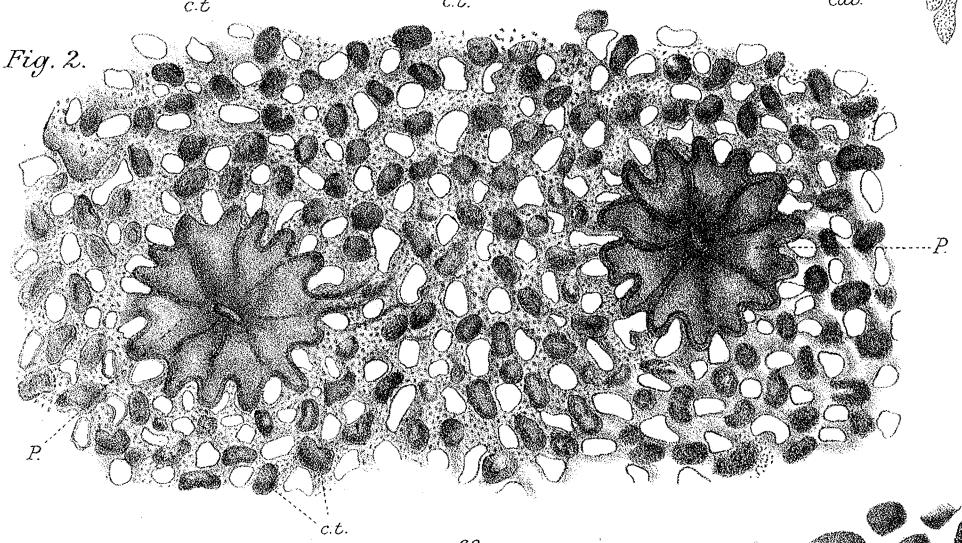


Fig. 4.

Fig. 2.



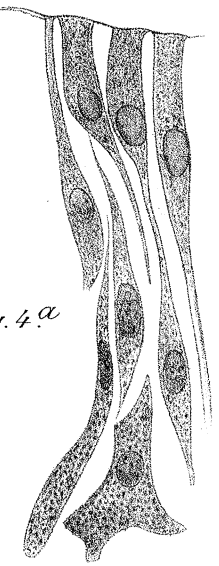


Fig. 4 a

Fig. 5.

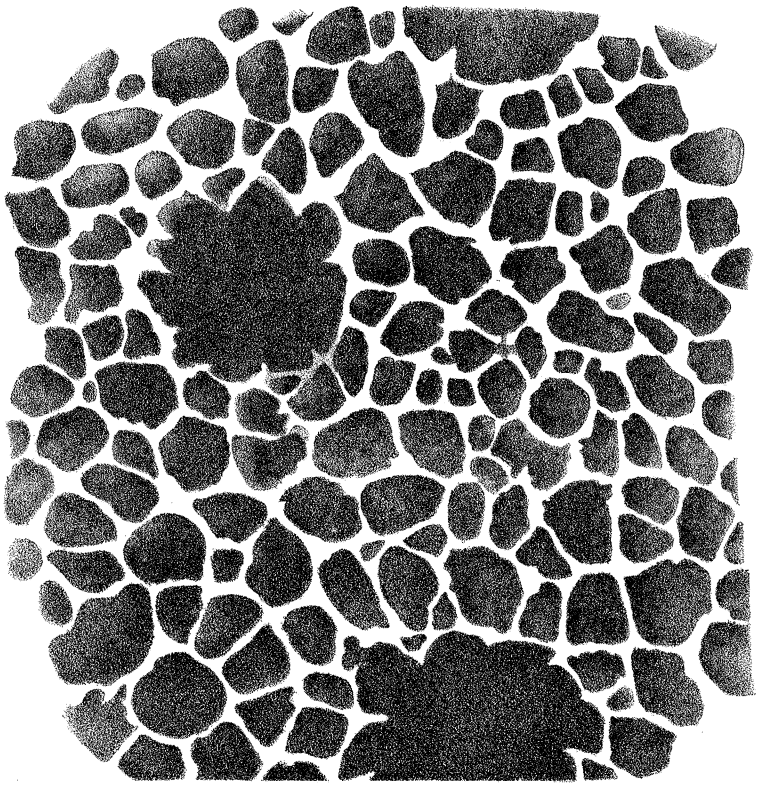


Fig. 3.

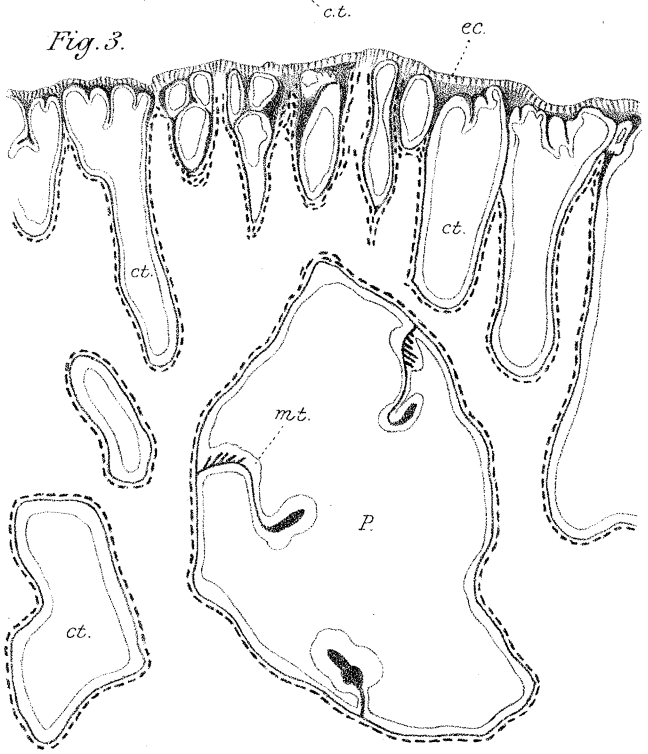


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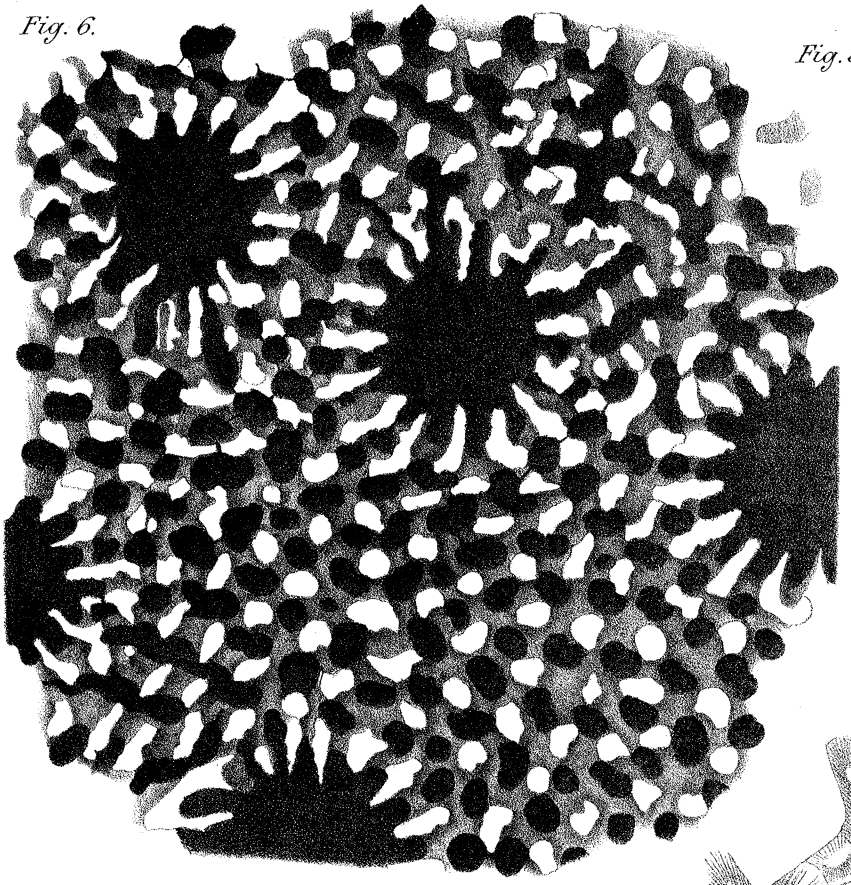
Fig. 6.



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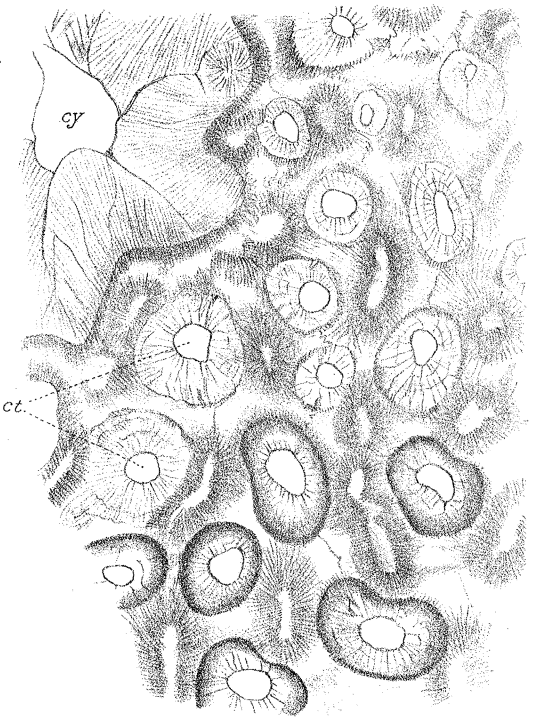

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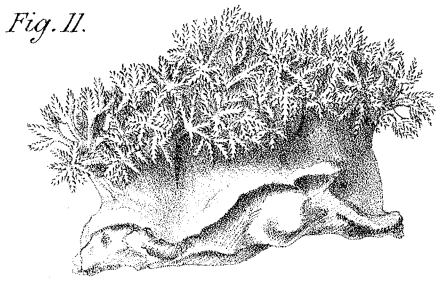

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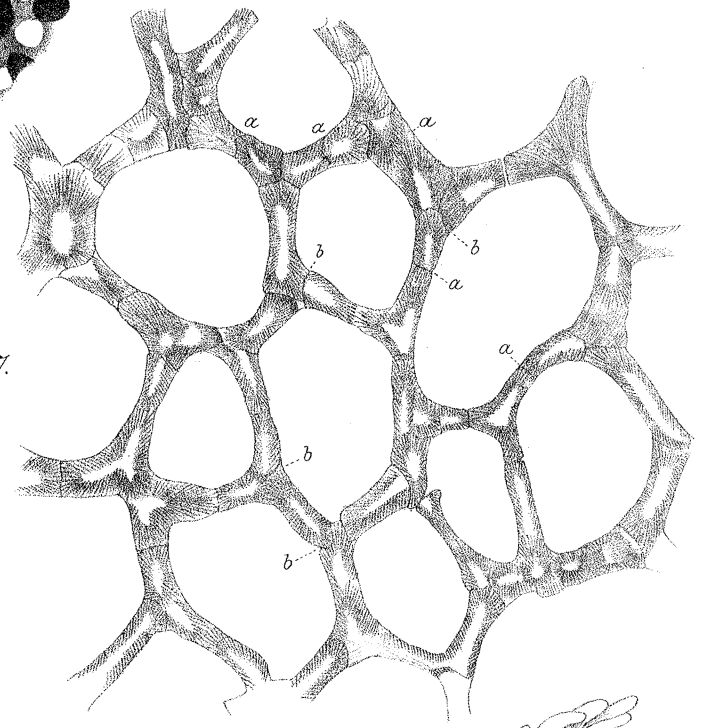

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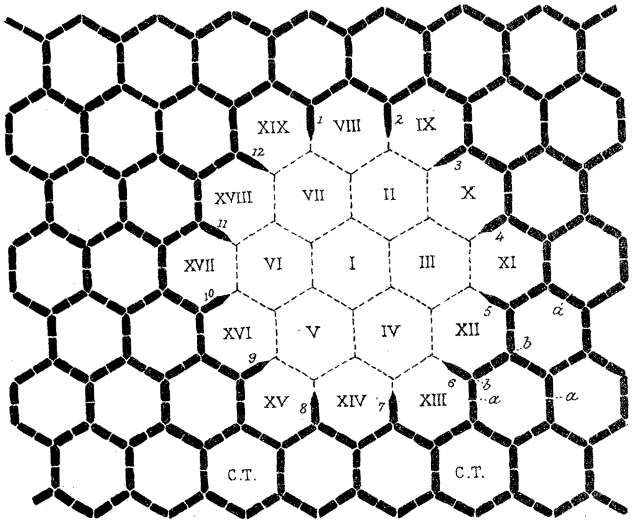

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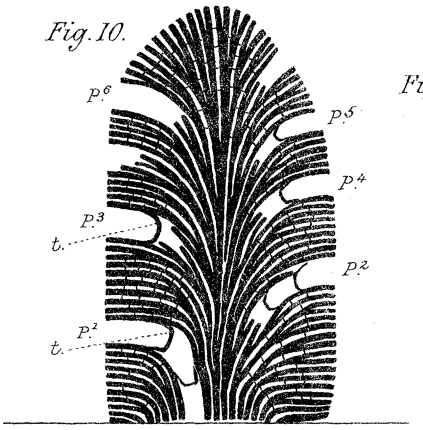


Fig. 11.a

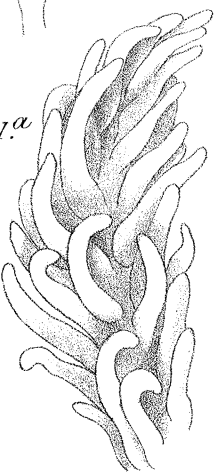


Fig. 14.

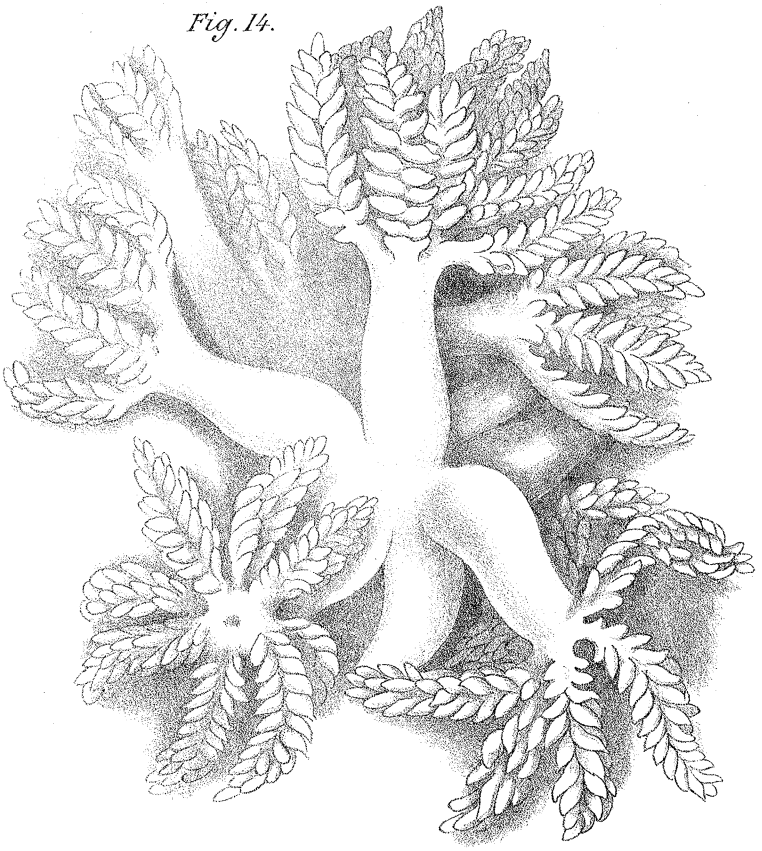


Fig. 15.

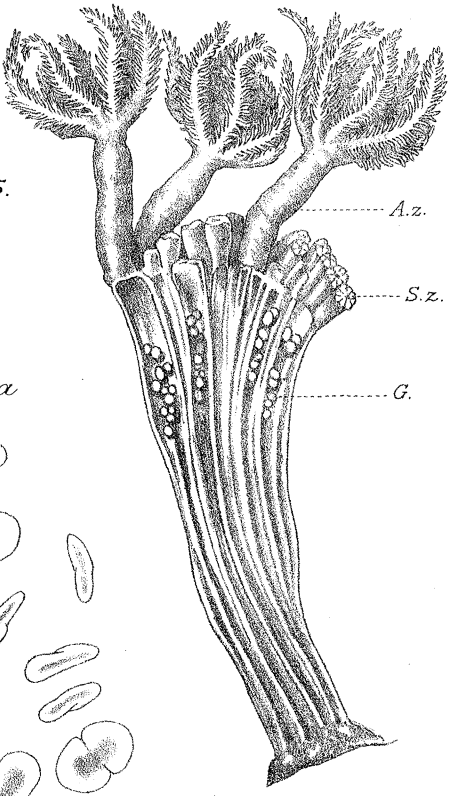


Fig. 15.a

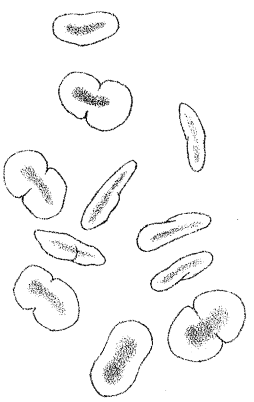


Fig. 12.

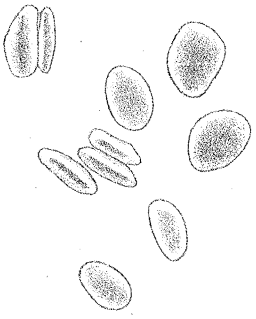


Fig. 13.

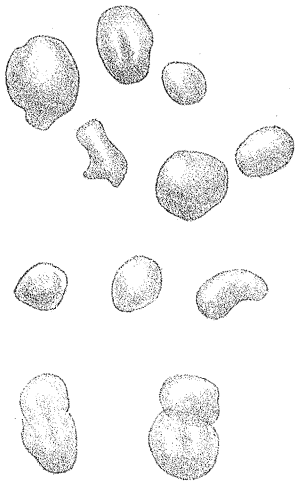


Fig. 16.

Fig. 17.

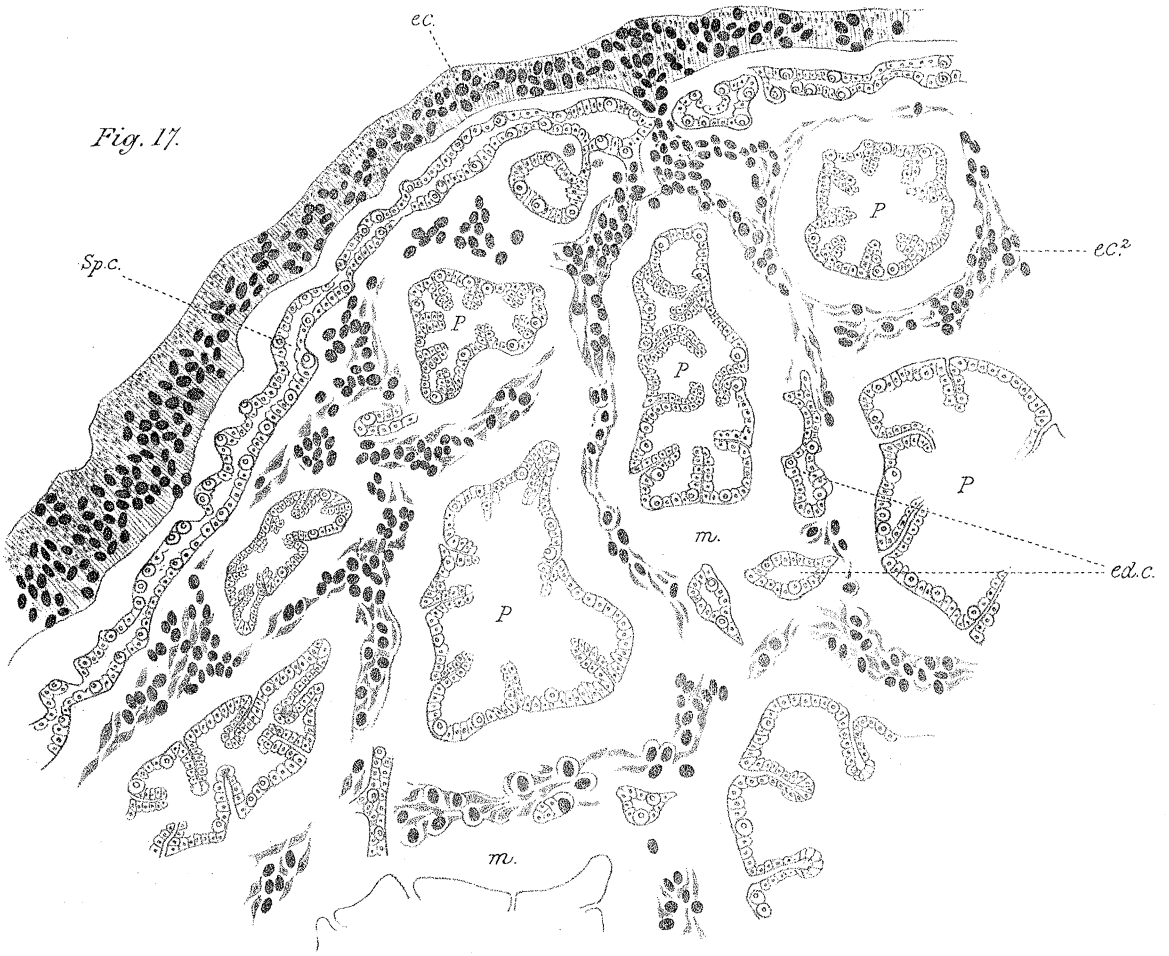
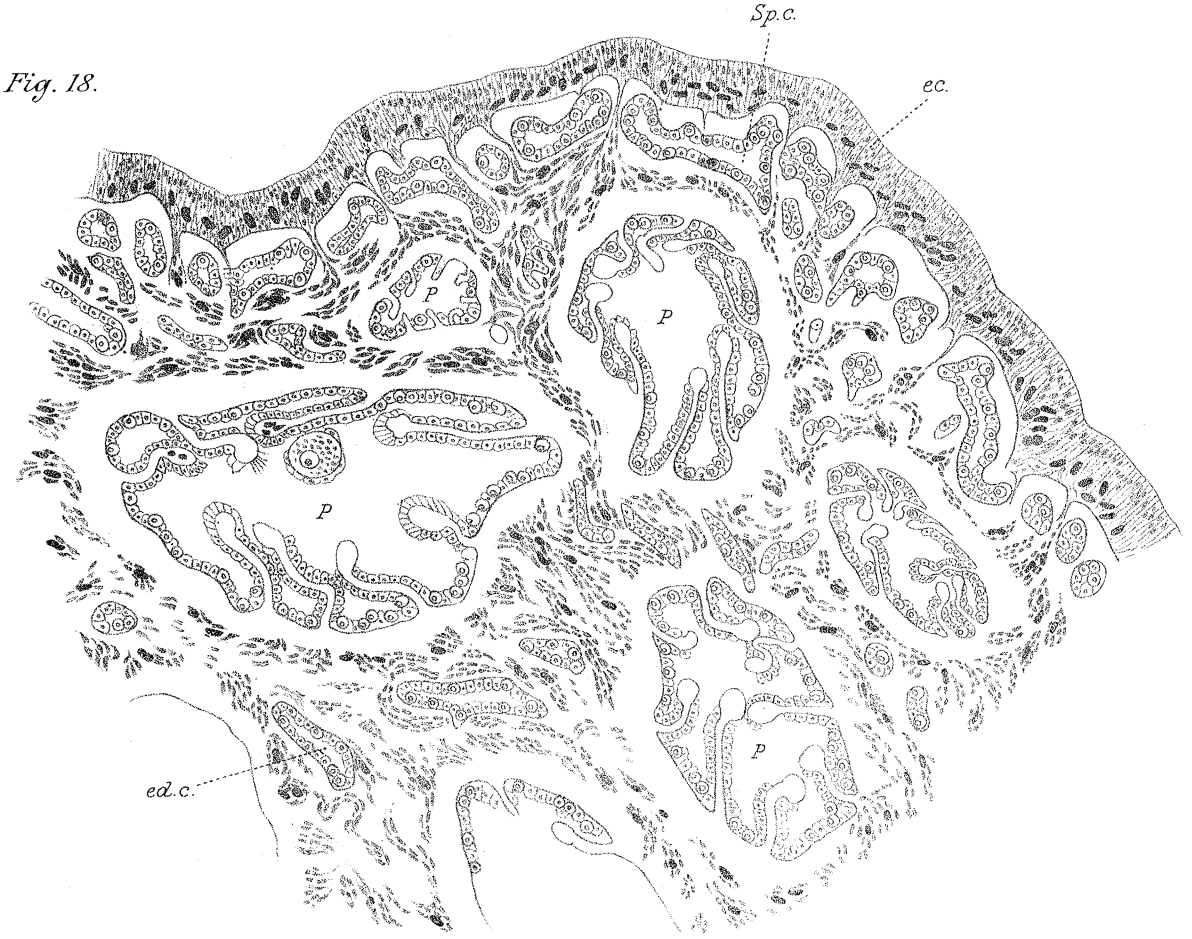
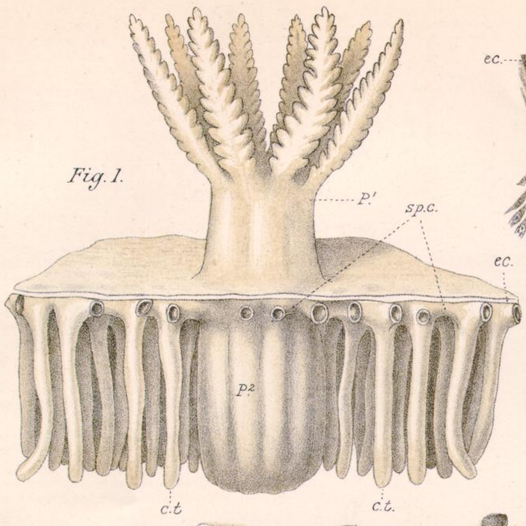
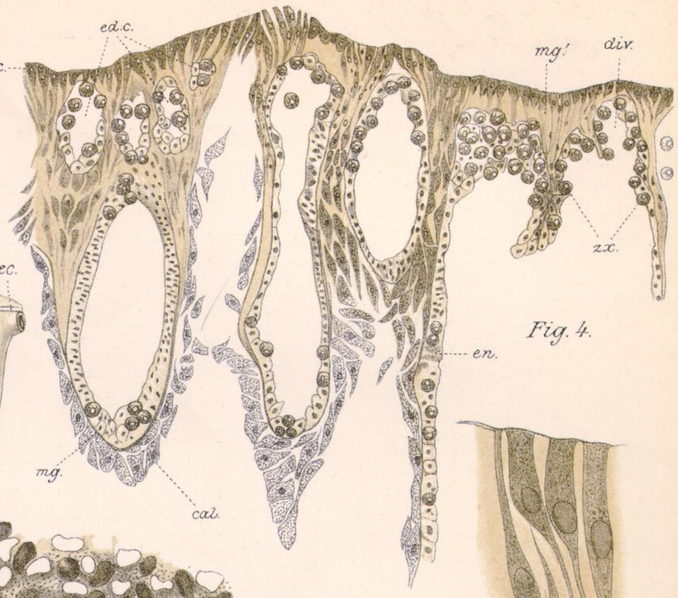
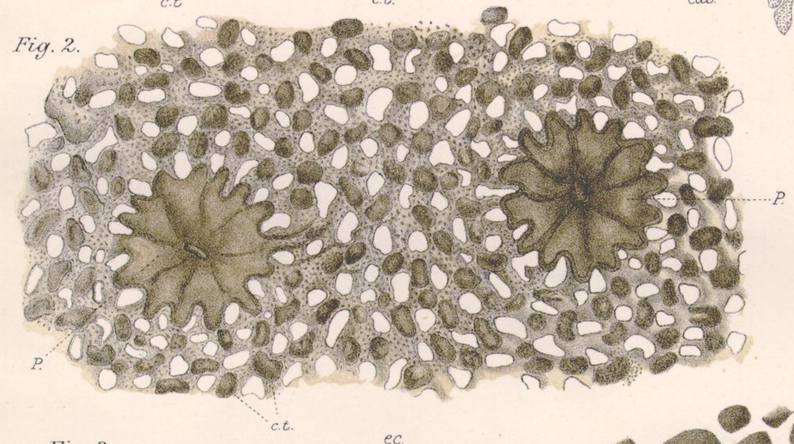


Fig. 18.









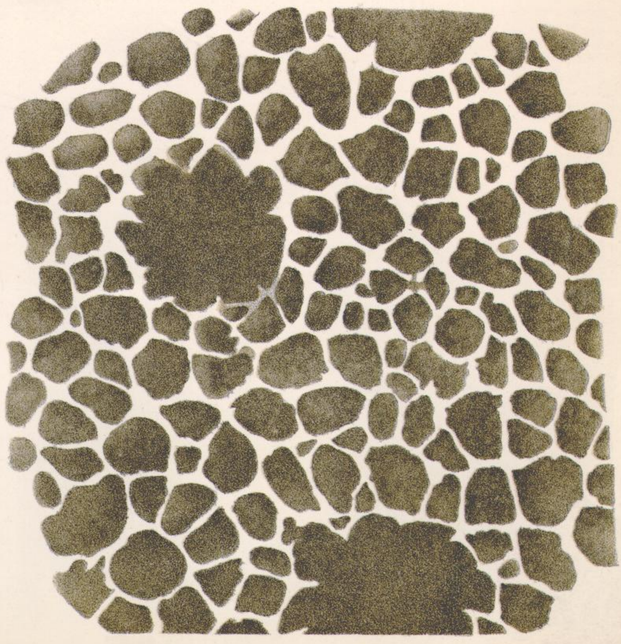


PLATE 10.

Fig. 1. A single polyp with the adjacent soft tissues of *Heliopora*, as seen after removal of the skeleton by decalcification. Partly diagrammatic. P^1., the exsert moiety of an expanded polyp, bearing eight pinnate tentacles. P^2., the proximal insert moiety of the same. *ec.*, the continuous sheet of ectoderm which clothes the whole surface of the colony. *sp.c.*, superficial canal system lying directly beneath the ectoderm. *ct.*, cœnenchymal cæca.

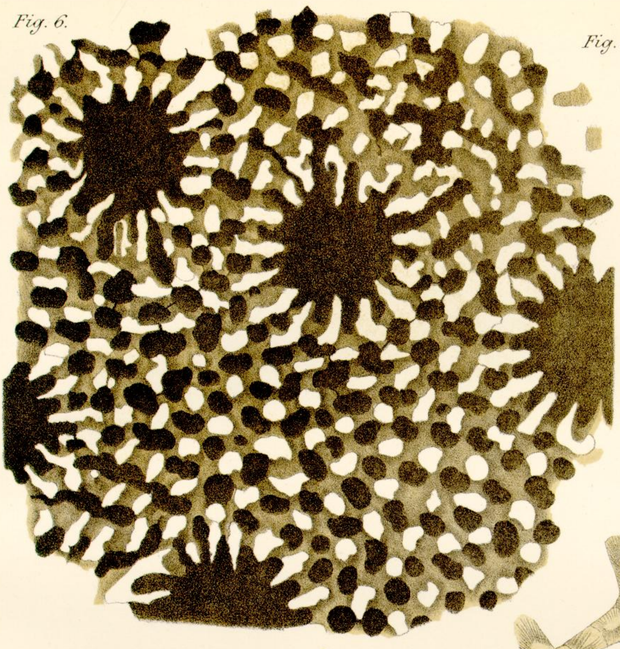
Fig. 2. Portion of a decalcified colony of *Heliopora cærulea* viewed from above. The superficial ectoderm has been stripped away exposing the superficial network of canals. Two retracted polyps are seen at *P.P.* in which it is obvious that there is no correspondence between the mesenteries and the pseudoseptal invaginations. The cœnenchymal cæca, *ct.*, are seen in optical section.

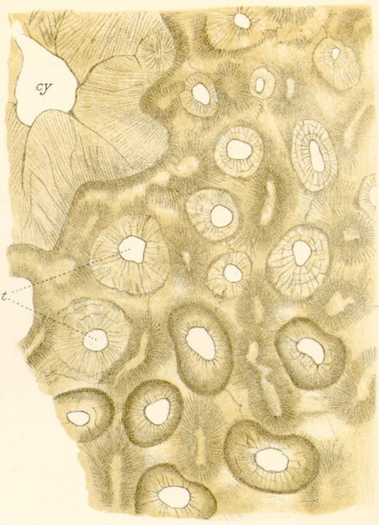
Fig. 3. Part of a vertical section through the soft tissues at the growing edge of a frond of *Heliopora*. The outlines are drawn in with a camera lucida; the details are filled in diagrammatically, the mesoglœa in dark line or shadow, the endoderm in light shadow. The discontinuous lines and dots represent the calicoblasts. *ec.*, superficial ectoderm. *ct.*, cœnenchymal cæca. *P.*, a polyp cavity. *mt.*, mesenteries.

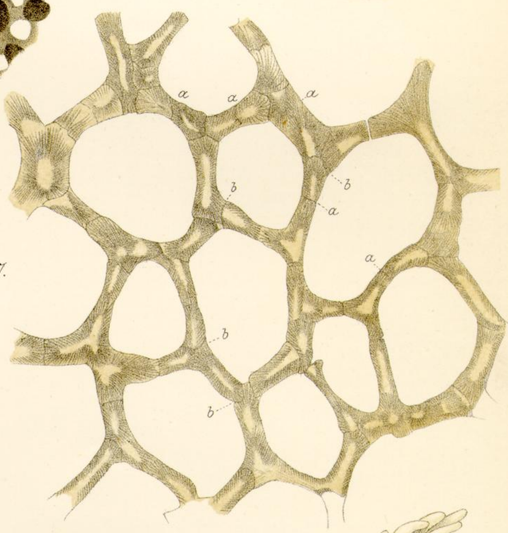
Fig. 4. A portion of the above section more highly magnified. *ec.*, ectoderm. *mg.*, definite layer of mesoglœa in the wall of a cœnenchymal cæcum. *mg'.*, mesoglœa in process of formation from the ectoderm. *en.*, endoderm lining a cœnenchymal canal. *ed.c.*, outgrowths of endoderm into the newly-formed mesoglœa. *zx.*, zooxanthellæ. *div.*, diverticula of a cœnenchymal cæcum. *cal.*, calicoblasts.

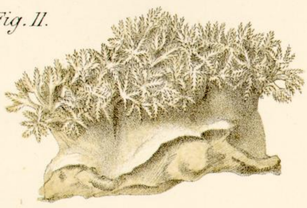
Fig. 4A A group of proliferating ectoderm cells, highly magnified.

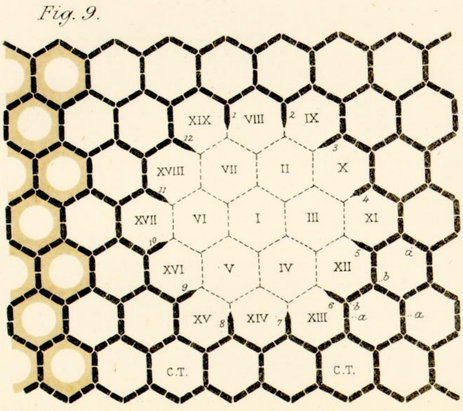
Fig. 5. Surface view of the hard tissues of the growing edge of a frond of *Heliopora*. Zeiss, A.A., Oc. 2.











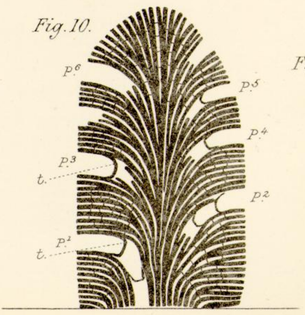


PLATE 11.

Fig. 6. Surface view of a fully-grown portion of a colony of *Heliopora*, showing the calicles, with their pseudosepta, the cœnenchymal fenestræ, the superficial echinulations, and the shallow canals between them in which the superficial canals lie.

Fig. 7. Portion of a tangential section through the growing edge of the corallum of *Heliopora*. *b.b.*, point to the union of three calcareous lamellæ to form a triradiate figure. *a.a.*, point to the sutures connecting the arms of adjacent triradial figures.

Fig. 8. Portion of a section parallel to the surface of an older portion of a colony of *Heliopora*. *cy.*, calicle, around the diminished cavity of which is a thick secondary deposit. *ct.*, cœnenchymal tubes whose cavities are partially occluded by annular secondary deposits. Between them is seen the trabecular skeleton which was first formed at the growing edge of the frond. The dark lines round the cœnenchymal tubes in the lower part of the figure show the concentration of the blue colouring matter of the corallum in definite zones.

Fig. 9. Diagram illustrating the essential structure of the corallum in *Heliopora* and *Heliolites*. *C.T.*, cœnenchymal tubes, the walls of each of which are composed of 12 separate laminæ which take a share in the composition of the walls of six adjacent tubes. *a.a.*, *b.b.*, as in fig. 7. In the centre of the figure a calicular cavity is indicated, formed by the arrest, complete or partial, of a group of 19 cœnenchymal tubes, numbered I.–XIX. The outlines of the arrested tubes are shown by dotted lines. The pseudosepta, 1–12, are seen to be formed from the walls of the circumferential partially arrested tubes, viz., VIII.–XIX. To the left, the secondary deposits formed within the cœnenchymal tubes of *Heliopora* are indicated.

Fig. 10. Diagram illustrating the mode of growth and architecture of a colony of *Heliopora cærulea*. The arrangement shown in the diagram may easily be followed in a vertical section through a frond of *Heliopora cærulea*. P', mother polyp, from which the colony has been developed. P^2, P^3, etc., daughter polyps successively formed among the cœnenchymal tubes. The centre of the colony is seen to consist of generally vertical ascending tubes. As fresh tubes are added among their upper ends, they are successively pushed out of the vertical and come to take a horizontal position. In the diagram, the black lines represent the skeleton, the cavities are left white. *t.t.* tabulæ.

Fig. 11. A colony of *Xenia umbellata var. cærulea*. Natural size.

Fig. 11A. A tentacle of the same magnified, to show the pinnæ.

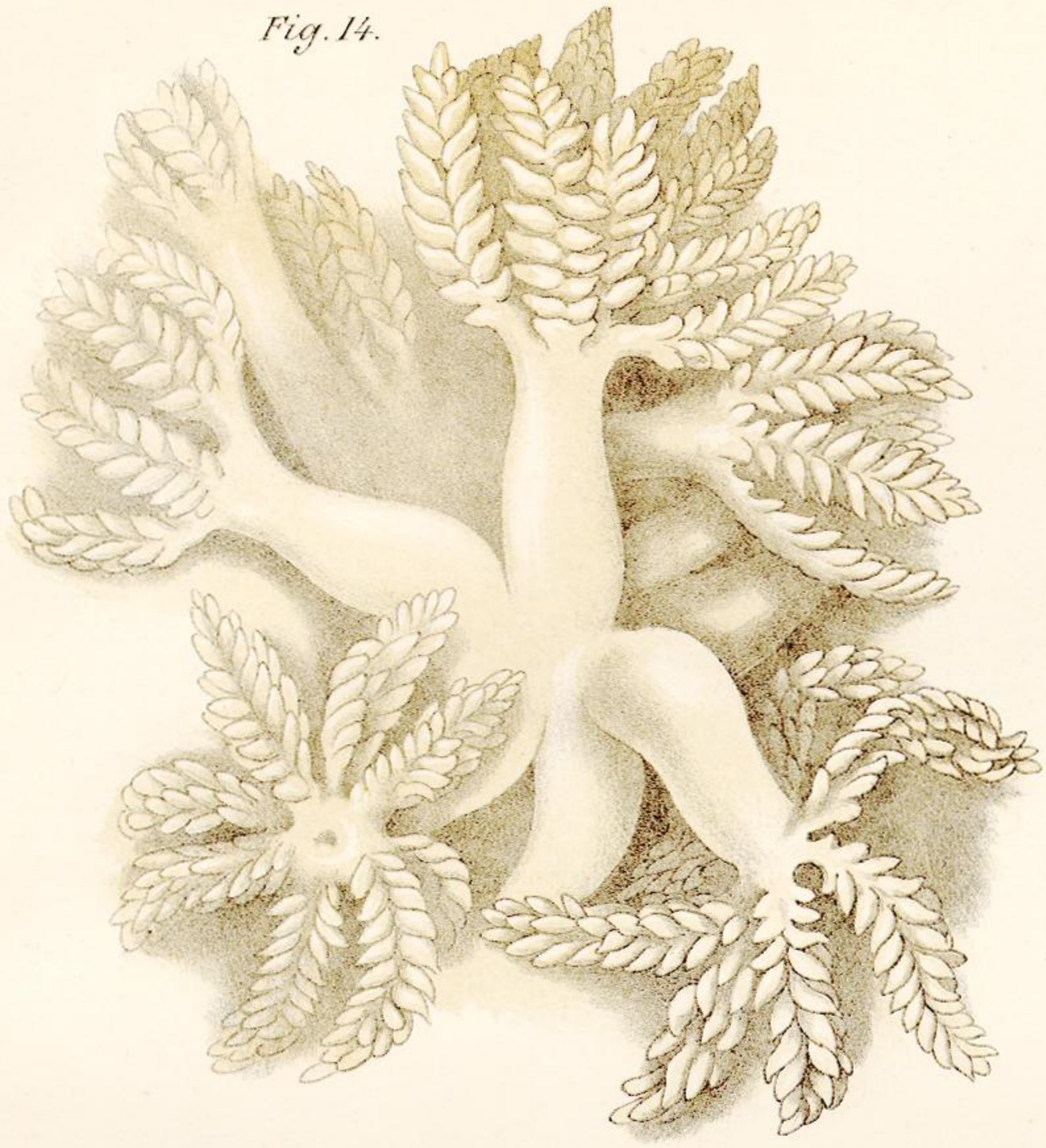


Fig. 14.

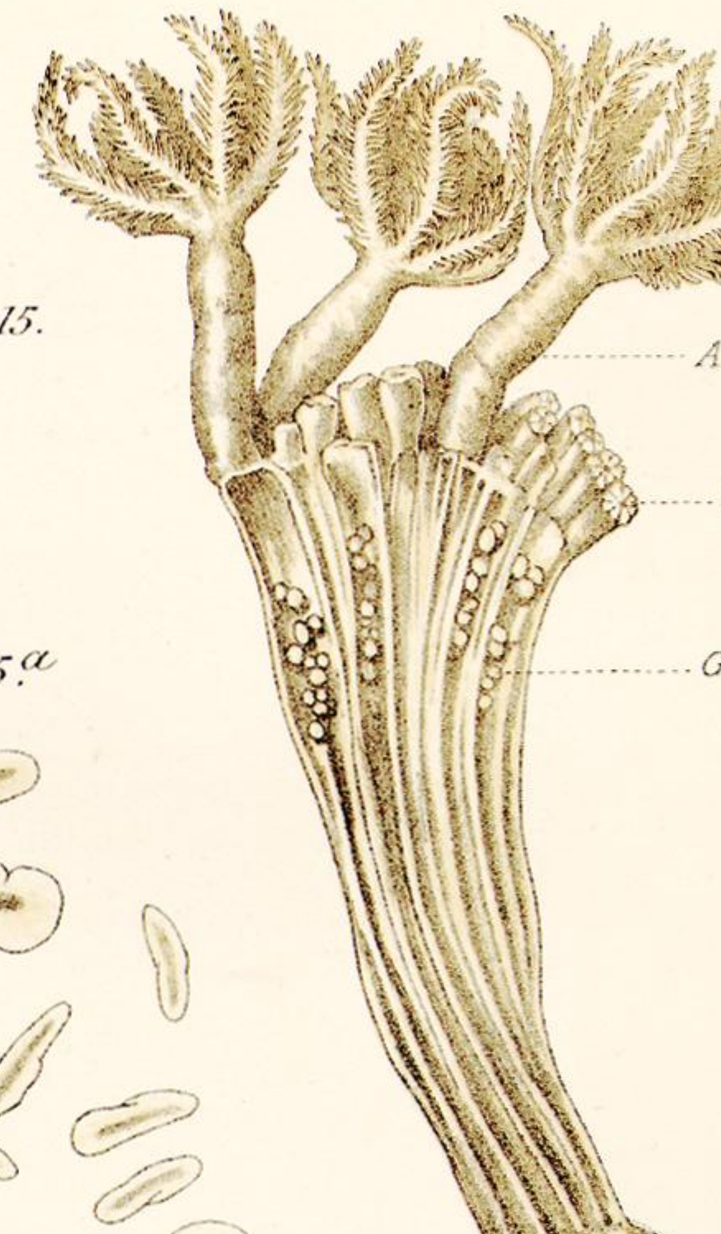


Fig. 15.

Fig. 15a

Fig. 12.

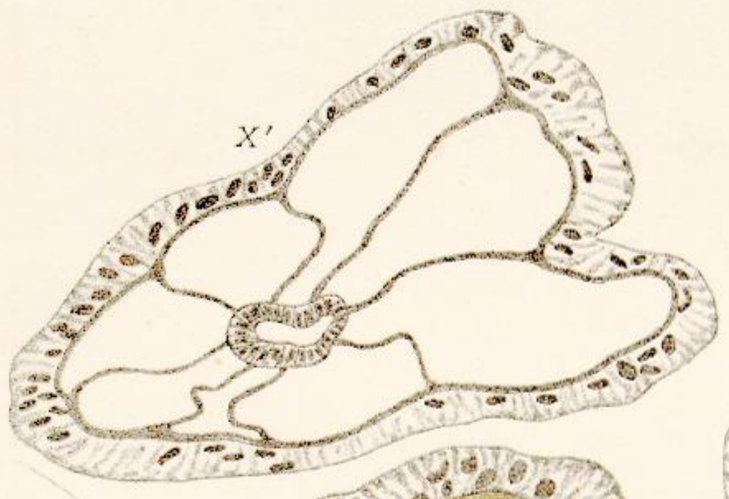


Fig. 16.

Fig. 13.

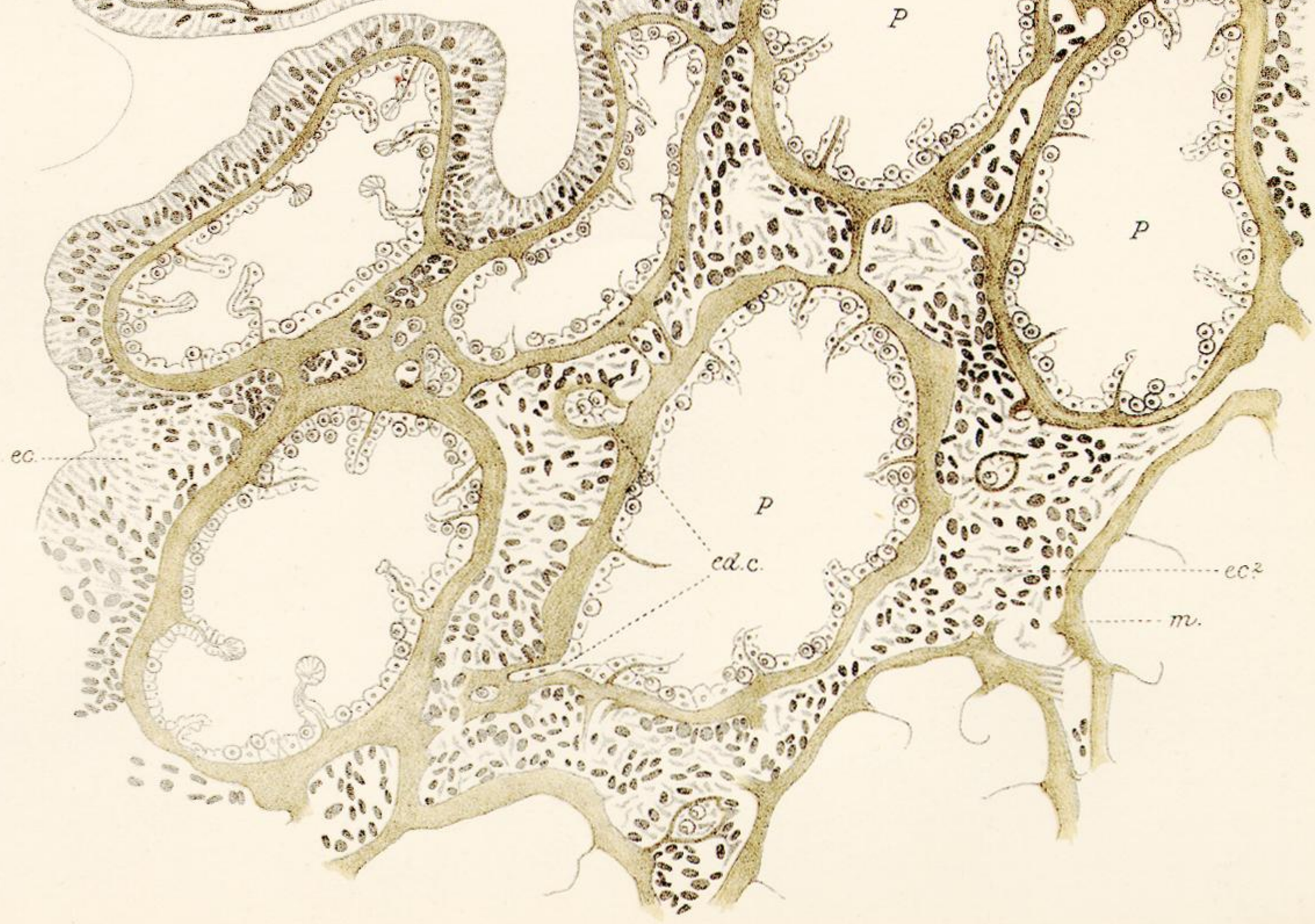


PLATE 12.

Fig. 12. Spicules of *Xenia umbellata*. Zeiss, D., Oc. 4.

Fig. 13. Spicules of *Xenia Garciæ*. Zeiss, D., Oc. 4.

Fig. 14. A group of polyps from a colony of *Xenia Garciæ*, magnified, to show the pinnæ.

Fig. 15. Drawing of a part of a colony of *Heteroxenia Elizabethæ*, which has been cut in half vertically. *Az.*, autozooids. *Sz.*, siphonozooids. *G.*, gonads in the cavities of the autozooids.

Fig. 15a. Spicules of *Heteroxenia Elizabethæ*. Zeiss, D., Oc. 4.

Fig. 16. Part of a transverse section through the stem of *Xenia umbellata*. *P.*, polyp cavities with mesenteries. *ec.*, ectoderm covering the surface of the colony. *ec²*., ectoderm forming the cœnenchymal mass in which the polyp cavities are embedded. *ed. c.*, endodermic canals. *m.*, mesogloea. Zeiss, B., Oc. 2. (In this and the two next figures, the general features are drawn in accurately with the camera lucida. The spicules which appear as dark spots, looking like nuclei, are shown in their proper proportion and situation, but the details of ectoderm and endoderm are filled in diagrammatically, the size of their cells being too small to be satisfactorily represented under the low magnification.)

Fig. 17.

Fig. 18.

PLATE 13.

Fig. 17. Part of a transverse section through the stem of *Xenia Garciæ*. *sp. c.*, superficial endodermic canals. The remainder of the lettering as in fig. 16.

Fig. 18. Part of a transverse section through the stem of *Heteroxenia Elizabethæ*. The polyp cavities are embedded in a mass of homogeneous mesoglœa, which is penetrated by numerous strands of ectodermic tissue some of the cells of which develop spicules. Lettering as before.